

# CRETACEOUS FAUNAS FROM ZULULAND, SOUTH AFRICA, AND SOUTHERN MOZAMBIQUE THE APTIAN ANCYLOCERATIDAE (AMMONOIDEA)

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(With 89 figures)

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## ABSTRACT

Heteromorph ammonites referred to the subfamilies Ancyloceratinae, Heteroceratinae, and Helicancylinae occur widely in rocks of Aptian age in northern Zululand and southern Mozambique. The subfamily Ancyloceratinae is represented by *Ancyloceras* (*Ancyloceras*), *Ancyloceras* (*Adouliceras*), *Tropaeum*, *Australiceras* and a specimen tentatively referred to *Lithancylus*. The subfamily Helicancylinae, separated from the Ancyloceratinae with some hesitation, is represented by *Toxoceratoides* and *Tonohamites* although doubt exists as to the generic affinity of some of the species. The subfamily Heteroceratinae is represented in the Upper Aptian by a helical hamitid-like form with or without tubercles, referred to a new genus, *Helicancyloceras*. Dimorphism is tentatively recognized in *Ancyloceras* (*Adouliceras*) and *Helicancyloceras*, whilst observations on the biogeography of the group are also included.

The following new species are described: *Ancyloceras* (*Adouliceras*) *cooperi* sp. nov., *Tropaeum* *dayi* sp. nov., *Tropaeum* *obesum* sp. nov., *Australiceras* *wandalina* (Boshoff MS) sp. nov., *Toxoceratoides*? *haughtoni* sp. nov., *Tonohamites*? *caseyi* sp. nov., *Helicancyloceras* (*Helicancyloceras*) *densecostatum* sp. nov., *Helicancyloceras* (*Nonyaniceras*) *nonyani* sp. nov., *Helicancyloceras* (*Nonyaniceras*) *circulare* sp. nov. and *Helicancyloceras* (*Nonyaniceras*) *crassetuberculatum* sp. nov.

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## INTRODUCTION

Ammonites belonging to the family Ancyloceratidae are locally abundant in the Aptian of northern Zululand and southern Mozambique. Most specimens are fragmentary, and complete individuals rare, making positive identifications difficult in many instances. In the descriptions given below, the authors have in consequence made extensive use of open nomenclature in the sense of Richter (1948; see also Matthews 1973).

The family Ancyloceratidae is represented by the following subfamilies in the present collection: Ancyloceratinae Meek, 1876, Heteroceratinae Spath, 1922, and Helicancylinae Hyatt, 1900. Some of the Heteroceratinae have been described elsewhere (Klinger 1976).

The subfamilies of the Ancyloceratidae are all intimately related, and some may be superfluous; the authors retain them here as a working framework for classification of their material, for they do seem to show a reasonable degree of morphological homogeneity, and are of value when dealing with fragmentary material, as Thomson (1974: 17) has noted. Extensive splitting of the heteromorphs at family level, as suggested by Dimitrova (1970), is to be avoided in the authors' view, given the current state of knowledge of several groups which is still insufficient for a confident statement of their phyletic relationships, especially as many classic species require reinvestigation.

The Ancyloceratidae have a world-wide distribution and, following the systematic account, the authors give details of the palaeobiogeography of the group.

Generic comparisons may be drawn on a global scale, but at specific level most of the taxa encountered in the literature appear of more limited distribution, and some are markedly endemic. A close relationship exists, however, between the Barremian and Aptian faunas of Zululand and southern Mozambique and those of the southern U.S.S.R. as shown below, and as noted recently by Förster (1975a: 256, 1975b: 270).

The following species are described below:

*Ancyloceras?* sp. ind.

*Ancyloceras?* sp. cf. *humboldtiana* (Lea)

*Ancyloceras* (*Adouliceras?*) sp. cf. *ajax* Anderson

*Ancyloceras* (*Adouliceras*) *mozambiquense* (Krenkel)

*Ancyloceras* (*Adouliceras*) *cooperi* sp. nov.

*Ancyloceras* (*Adouliceras*) sp. gr. ex. *mozambiquense* (Krenkel)—*cooperi* sp. nov.

*Lithancylus* sp.

*Tropaeum* sp. aff. *subsimbirskense subsimbirskense* (Sinzow)

*Tropaeum subsimbirskense compressum* (Sinzow)

*Tropaeum rossicum* Casey

*Tropaeum dayi* sp. nov.

*Tropaeum obesum* sp. nov.



- Tropaeum* sp. aff. *undatum* Whitehouse  
*Tropaeum* sp. gr. ex. *bowerbanki* J. de C. Sowerby *densistriatum*  
     Casey—*hillsi* (J. de C. Sowerby)  
*Tropaeum* sp. indet.  
*Australiceras ramososeptatum* (Anthula)  
*Australiceras* sp. aff. *irregulare* (Tenison Woods)  
*Australiceras wandalina* (Boshoff MS) sp. nov.  
*Australiceras* spp. indet.  
*Australiceras* sp. cf. 'Crioceras' *sarasini* Favre  
*Toxoceratoides royerianus* (d'Orbigny)  
*Toxoceratoides krenkeli* Förster  
*Toxoceratoides? haughtoni* sp. nov.  
*Tonohamites koeneni* Casey  
*Tonohamites* sp. aff. *aequicingulatus* (von Koenen)  
*Tonohamites? caseyi* sp. nov.  
*Helicancyloceras (Helicancyloceras) vohimaranitraensis* (Collignon)  
*Helicancyloceras (Helicancyloceras) densecostatum* sp. nov.  
*Helicancyloceras (Helicancyloceras) spp.* indet.  
*Helicancyloceras (Nonyaniceras) nonyani* sp. nov.  
*Helicancyloceras (Nonyaniceras) circulare* sp. nov.  
*Helicancyloceras (Nonyaniceras) crassetuberculatum* sp. nov.  
*Helicancyloceras (Nonyaniceras) spp.* fragments  
*Incertae sedis.*

#### LOCATION OF SPECIMENS

The following abbreviations are used to indicate the source of the material:

- |        |  |
|--------|--|
| SAS    | Geological Survey of South Africa, Pretoria    |
| SAM    | South African Museum, Cape Town                |
| UPG    | Department of Geology, University of Pretoria  |
| BM(NH) | British Museum (Natural History), London       |
| NMB    | National Museum, Bloemfontein                  |
| OUM    | University Museum, Oxford                      |
| UP     | Palaeontological Institute, Uppsala University |
| MNHP   | Muséum d'Histoire Naturelle, Paris.            |

#### FIELD LOCALITIES

Details of field localities referred to in this paper are given by Kennedy & Klinger (1975). Co-ordinates of additional localities in Zululand studied since then, and localities in southern Mozambique collected by M. R. Cooper are provided in the text.

## MEASUREMENTS

Dimensions of specimens are given in millimetres; abbreviations are as follows:

D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter.

Figures in parentheses are dimensions expressed as a percentage of the total diameter. As no standard set of abbreviations for heteromorph ammonoids has as yet come into common use, other dimensions are written out in full.

## SYSTEMATIC PALAEOLOGY

Class	CEPHALOPODA Zittel, 1884
Order	AMMONOIDEA Zittel, 1884
Suborder	ANCYLOCERATINA Wiedmann, 1966
Superfamily	ANCYLOCERATACEAE Meek, 1876
Family	<b>Ancyloceratidae</b> Meek, 1876
Subfamily	Ancyloceratinae Meek, 1876.

The features which allow separation of the Ancyloceratinae and Crioceratitinae are very slight indeed. Casey (1960) accorded the Ancyloceratinae and Crioceratitinae subfamilial rank. His extensive researches on the heteromorphs of the English Lower Greensand (Aptian to Lower Albian) have contributed enormously to our knowledge of these ammonites, and without his work the description of the Zululand and Mozambique species would have been rendered much more difficult. In view of this, the subfamilies are separated here also, although the differences in features which allow their distinction are slight.

The Ancyloceratinae are not well represented in the Cretaceous of Zululand and southern Mozambique, but few other ammonite groups present in the area grow to such enormous sizes and show such distinctive and bizarre coiling.

The subfamily is represented by the following genera: *Ancyloceras* s.l. d'Orbigny, 1842, *Tropaeum* J. de C. Sowerby, 1837, *Australiceras* Whitehouse, 1926, and *Lithancylus* Casey, 1960.

Genus *Ancyloceras* d'Orbigny, 1842*Type species*

*Ancyloceras matheronianum* d'Orbigny, 1842 from the Lower Aptian of France by the subsequent designation of Haug (1889: 212).

*Diagnosis*

Small to large heteromorphs with ancyloceratid coiling; early whorls in contact or widely separated. Ornament consists of trituberculate ribs separated

by a variable number of intermediate non-tuberculate ribs throughout, or only in early and late growth stages.

Subgenus *Ancyloceras* (*Ancyloceras*) d'Orbigny, 1842

*Diagnosis*

*Ancyloceras* in which trituberculate ribs are present throughout ontogeny.

*Discussion*

The genus *Ancyloceras* has become a receptacle for many heteromorphs showing ancyloceratid coiling, and as Casey (1960: 21) indicated, most of the Georgian (Gruzinian) ancyloceratids described by Rouchadzé (1933) are generically distinct from *Ancyloceras* and should probably be referred to *Pedioceras* or some genus within the *Pedioceratinae*. The same holds true for some ancyloceratid forms from the U.S.S.R. and from Bulgaria described by Drushchitz & Kudryavtsev (1960) and Dimitrova (1967) respectively. Inasmuch as the family *Pedioceratidae* is not well defined, and *Pedioceras* is a poorly-known genus (Yenne 1949 provides the most comprehensive discussion), it is perhaps wisest to retain the forms noted above in *Ancyloceras* with a mark of interrogation.

*Ancyloceras* (*Ancyloceras*?) sp. indet.

Figs 1A–B, 18B, 79D

*Material*

SAS H54/39 and SAS B11 from the Lower Aptian of Locality 170, Zululand.

*Description*

Only part of the initial coil and a non-septate fragment are known. Initial coiling appears to have been relatively close, with the whorls just touching, but not impressed. In SAS B11 (Fig. 1A–B) the two coils are not in one plane, but are helicoid. This does not appear to be due to postmortem damage. The whorl section is ovoid, wider than high (i.e. lateral diameter greater than siphonal–antisiphonal diameter) with a broadly rounded venter and dorsum. Ornament consists of major trituberculate ribs and a varying number (usually one to three) of intermediaries. The tubercles are very prominent and were originally spinose, and where the spines have broken off, low, round bosses remain, indicating the presence of a basal septum separating spine from shell.

The suture line is too poorly preserved for comment.

*Dimensions*

Specimen	D	Wb	Wh	Wb/Wh	U
SAS B11	c. 36	16,5(c. 49)	12,6(c. 20)	1,3	17(c. 47)



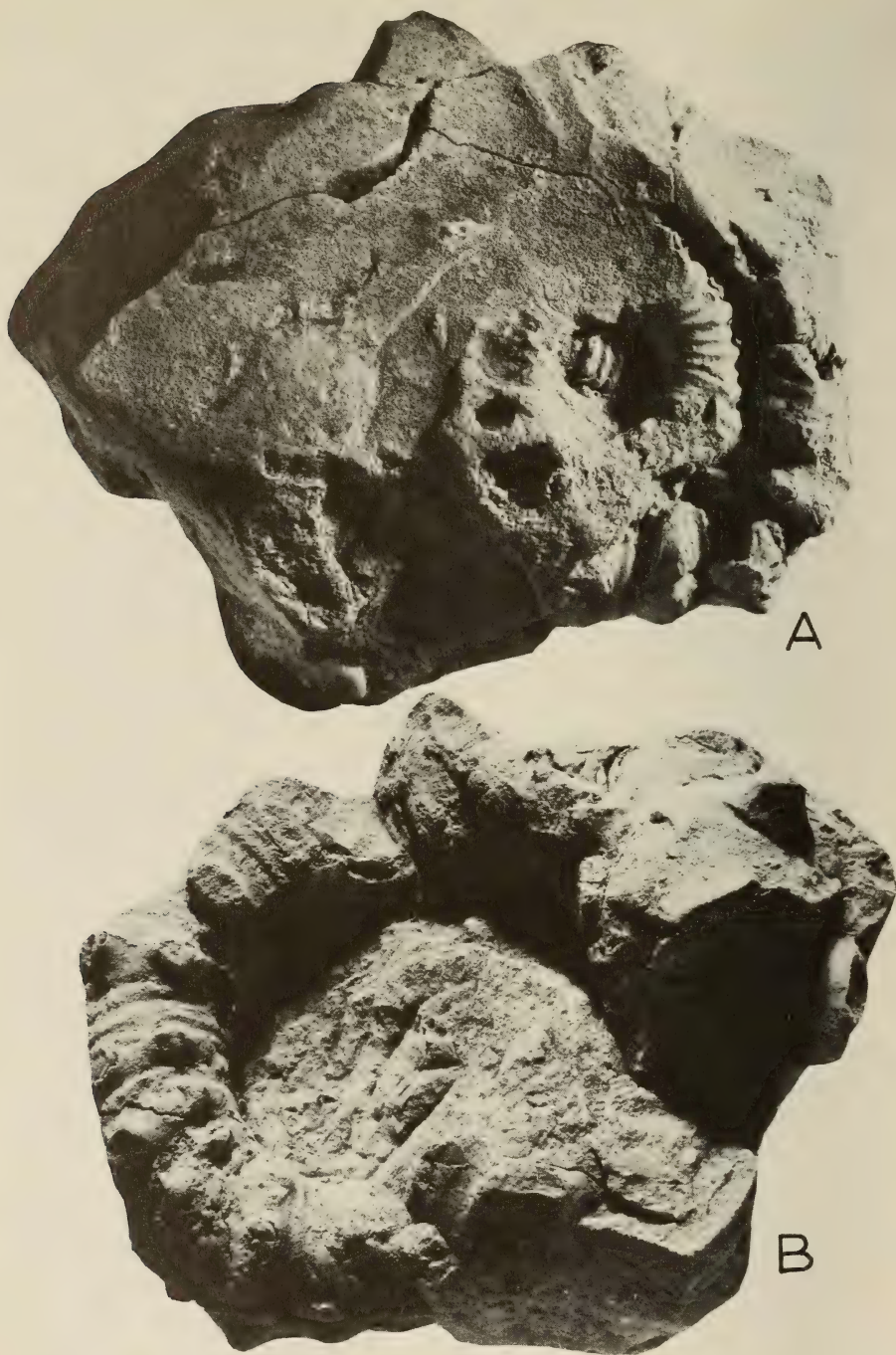


Fig. 1. A-B. *Ancyloceras* (*Ancyloceras*?) sp. indet. Dorsal and lateral views of specimen SAS B11 from locality 170, Aptian I.  $\times 1,5$ .

### Discussion

This is one of the few ammonites known in Bed 43 at locality 170 (see Kennedy & Klinger 1975, fig. 11). The fact that the coils in specimen SAS B11 are not in one plane, but rather appear helical, is disturbing. According to Clark (1958: 1076) the coiling in *Ancylloceras* is always planispiral, and is a feature (amongst others), which serves to distinguish *Ancylloceras* from *Anisoceras*. Unfortunately our material does not permit a more detailed investigation to determine whether coiling is helical throughout the species or merely restricted to this one specimen due to pathological reasons.

*Ancylloceras helicoides* Rouchadze (1933: 217, pl. 8 (fig. 3)) from Kouthais, Georgia (U.S.S.R.) is a helically coiled ancyloceratid, and is referred to a new genus, *Kutatissites*, by Kakabadze (1970). If the Zululand species is indeed coiled helically in all specimens, it should be referred to *Kutatissites*. This would further accentuate the close similarity between the Lower Cretaceous faunas of the southern part of the U.S.S.R. and south-eastern Africa.

Until further material becomes known the authors prefer to retain the species in the genus *Ancylloceras* with a mark of interrogation.

### Occurrence

Aptian I of Zululand.

*Ancylloceras?* sp. cf. *A. humboldtiana* (Lea, 1841)

Fig. 2

Compare:

*Ancylloceras humboldtiana* (Lea, 1841) in Forbes 1845: 171–172.

### Material

BMNH C79717 from locality 166, Mfongozi Creek, Zululand, Aptian III.

### Description

The single specimen consists of a fragment of the inner whorls and part of the outer whorl and straight shaft.

The inner whorl is ornamented by single, trituberculate ribs. On the outer whorl and shaft ribbing becomes sparse, and tuberculation weakened and possibly disappears. On the shaft the ribs are widely spaced with smooth interspaces.

### Discussion

Obviously specific identification based on this fragment alone is impossible. The Zululand specimen bears some similarity to the specimen figured by Forbes, in possessing widely-spaced ribs on the shaft, but differs in lacking the fine intermediary ribs.



Fig. 2. *Ancyloceras?* sp. cf. *A. humboldtiana* (Lea, 1841). BMNH C79717 from locality 166, Aptian III.  $\times 1$ .

*Occurrence*

Upper Aptian of Zululand.

Subgenus *Ancyloceras* (*Adouliceras*) Thomel, 1964

*Type species*

*Ancyloceras adouli* Astier, 1851 by the original designation of Thomel (1964: 56).

*Diagnosis*

Coiling ancyloceratid, generally with small initial spire, the whorls of which expand rapidly. Tubercles are linked by two or three ribs, but disappear



at varying diameters on the initial spire. Shaft generally ornamented by fine, dense ribs only, *without tubercles or differentiation into strong and weak ribs* for at least part of the length.

The crozier may be inflated and is generally ornamented by three strong rows of tubercles (lateral, lower and upper ventro-lateral) at some stage.

### Discussion

*Adouliceras* was erected as a subgenus of *Ancyloceras* by Thomel (1964: 55) with *Ancyloceras adouli* Astier, 1851 as type species. The holotype, BMNH C73806, reposit in the British Museum (Natural History), is here illustrated as Figures 3–4. Thomel's original diagnosis is as follows:

'Le sous-genre *Adouliceras*, créé pour les formes du groupe d'*Ancyloceras adouli* ASTIER, est caractérisé par une *spire à croissance très rapide*, à cette partie de la coquille, un port remarquable. L'ornementation de la spire est également particulière; elle consiste en côtes fines, simples toutes semblables, sur lesquelles on observe, de place en place, des tubercles, plus ou moins volumineux *à cheval sur deux ou trois consécutives*. La hampe, de section elliptique, est ornée de côtes simples, obliques, vigoureuses, généralement dépourvues de tubercules, du moins sur la partie cloisonnée. La crosse est connue seulement chez *A. adouli* ou elle porte des tubercules très vigoureux, et chez *A. renauxianum*.'

In addition to the type species, *A. kaliae* (Sarkar), *A. collignoni* (Sarkar) and *A. renauxianum* were referred to the subgenus. Comparison of *A. adouli* and *A. renauxianum* shows the extreme variation encountered in *A. (Adouliceras)*. In *A. (Ad.) adouli* the whorl section becomes abruptly inflated towards the hook. Furthermore, the initial spirally coiled section in the latter lacks tuberculation altogether. (See d'Orbigny 1842, pl. 123.) Whether this is in fact true, or merely another of d'Orbigny's artist's restorations is unknown.

Recently Murphy (1975) described a species from California under the name of *Ancyloceras thomeli*. In all respects this species has the characteristics of *Adouliceras*, apart from the fact that 'the spire of *A. thomeli* tapers much less rapidly than that of *A. adouli* which, according to Thomel (personal communication) is grounds for excluding the California form from *Adouliceras*' (Murphy 1965: 25). Comparison of the holotype of *A. (Ad.) adouli*, Figures 3–4, with the specimen figured by Thomel (1964, pl. 9 (fig. 2)) shows that the size of the initial spire is variable. This is further borne out by the Zululand and Mozambique material to be described below. The presence or absence of fine ribs on the hook quoted by Murphy as being a reason for separating *Ancyloceras thomeli* from *A. (Ad.) adouli* is just as variable.

It is here proposed to consider the absence of tubercles or stronger ribbing on part of the shaft and the mode of ornament on the early whorls as constituting the main characteristic of *Adouliceras*. The size of the initial spire is generally smaller than that of *Ancyloceras* s.s.



Fig. 3. *Ancyloceras* (*Adouliceras*) *adouli* Astier, 1851. BMNH C73806, the original of Astier (1851, pl. 6 (no. 12), pl. 7 (no. 12 bis)), from the Neocomian of Cheiron, Basses Alpes (France).  
 $\times 0,45$ .



Fig. 4. *Ancyloceras* (*Adouliceras*) *adouli* Astier, 1851. As in Figure 3.



In addition to the species mentioned above, the following may possibly also be referred to *Adouliceras*: *Ancyloceras attrox* Anderson (1938: 209 pl. 69 (figs 1–3)) and *Ancyloceras ajax* Anderson (1938: 210, pl. 65 (figs 1–3)). *Ancyloceras ewaldi* Dames (1880: 690, pl. 25, pl. 26 (fig. 1)) is probably also an example of *Adouliceras*.

*Adouliceras* represents a line of development which resembles that of *Australiceras* gr. ex. *gigas*, and some species were previously referred to that genus (e.g. Casey 1961: 51). Thomel (1964: 60, table 2), however, has shown that they are parallel but apparently unrelated lineages.

*Adouliceras* differs from *Ancyloceras* s.s. in lacking tubercles on part of the shaft. It differs from *Australiceras* gr. ex. *gigas* mainly in having a smaller initial spire, a different mode of tuberculation, looser coiling, and, most important of all, in lacking major costae and tubercles on the shaft. It may be distinguished from uncoiled species of *Tropaeum* e.g. *T.* gr. ex. *hillsi* by the possession of three rows of tubercles on the early and late parts of the shell. Non-tuberculate fragments of the ammonitic coils are generically indistinguishable from *Tropaeum*.

Unfortunately the South African and Mozambique material does not shed any light on the phylogeny and relationship of *Adouliceras* to other genera of the Ancyloceratinae.

#### Occurrence

Upper Barremian and Lower Aptian of western and central Europe, California, Zululand and Mozambique.

*Ancyloceras* (*Adouliceras*?) sp. cf. *ajax* Anderson, 1938

Figs 5–6A

Compare:

*Ancyloceras ajax* Anderson, 1938: 210, pl. 65 (figs 1–3).

#### Material

SAS Zo(1) from locality 162, Mfongozi Creek, Zululand. Lower ? Aptian.

#### Description

One large fragment consisting of the non-septate part of the shaft and crozier is compared to Anderson's species. The terminal septum is exposed at the broken end of the shaft.

The section of the shaft is ovoid, with a greater dorso-ventral than lateral diameter. Towards the crozier the whorl breadth increases rapidly, surpassing the whorl height. On the recurved end the whorl section is depressed with a flattened dorsum, moderately angular umbilical edge, and a broadly rounded venter.

Ornament on the shaft consists of low, rounded, oblique, prorsiradiate ribs. The ribs cross the dorsum with a slight forward curvature. The venter is abraded,



Fig. 5. *Ancyloceras* (*Adouliceras*) sp. cf. *ajax* Anderson, 1938. SAS Zo(n) from locality 162, Mfongozi Creek, Zululand, Lower? Aptian.  $\times 0,4$ .

but it appears that the ribs crossed the venter without diminution. There are about 25 ribs in a distance equal to the whorl height. At a point 70–80 mm before the bend in the crozier, strong ribs appear, becoming progressively stronger towards the bend. Umbilical, lateral and ventral tubercles develop on the major ribs. The major ribs cross the flanks radially and curve forward over the venter, but are effaced on the dorsum.

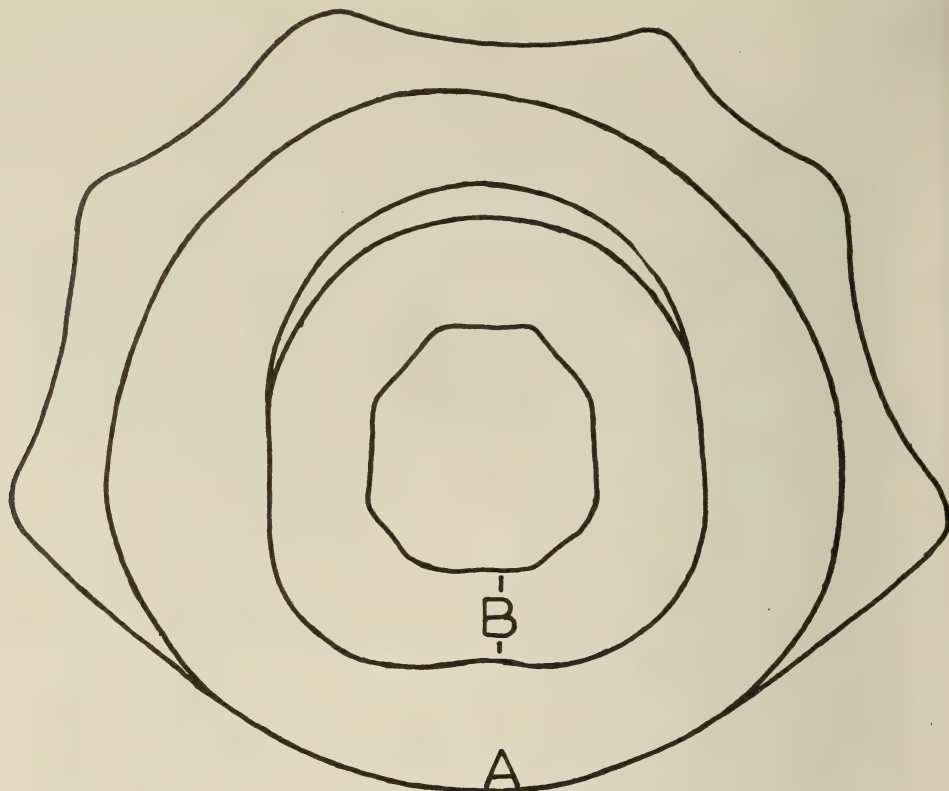


Fig. 6. A. Whorl section of *A. (Adouliceras)* sp. cf. *ajax* Anderson, 1938. SAS Zo(n).  $\times 1$ .  
 B. Whorl section of *Australiceras wandalina* sp. nov. UPG B8 from Manyola Drift, Aptian III.  $\times 0,5$ .

#### Dimensions

Wb	80	101,5	89,5
Wh	92,5	91,6	97,0
	End of shaft.	In crozier.	Aperture.

#### Discussion

The specimen bears a strong resemblance to the Californian *Ancylloceras ajax*, but lacks the inflated body chamber and the very strong tuberculation on the crozier.

*Ancylloceras thomeli* Murphy (1975: 24, pl. 3 (figs 1, 5), pl. 11 (figs 1–2)) also differs on account of the presence of an inflated body chamber.

In *A. (Ad.) renauxianum* d'Orbigny (1842: 499, pl. 123) non-tuberculate intermediaries occur between the major costae in the crozier. *A. (Ad.) ewaldi* Dames (1880: 690, pl. 25, pl. 26 (fig. 1)) has stouter ribbing on the shaft, and more closely spaced ribs on the crozier. *A. (Ad.) adouli* Astier (1851: 23, pl. 6 (nr 12); pl. 7 (nr 12b); see also Thomel 1964, pl. 9 (fig. 2)) has a strongly inflated body chamber and is readily distinguishable from the present specimen.



### Occurrence

The exact stratigraphic position of the Zululand specimen is unknown, although definitely Aptian. Anderson's species is said to come from close to the Barremian/Aptian boundary.

#### *Ancyloceras (Adouliceras) spp.*

##### group of *mozambiquense* Krenkel—*cooperi* nov.

Abundant leached concretions yielding fragments of ancyloceratids litter the surface and topsoil at locality 170. The stratigraphic interval represented by these concretions is at least 10 m, whilst similar material from Da Silva's (1962) locality A (26°49'50"S 32°12'55"E) herein referred to as Lubemba, in southern Mozambique is available. Apart from the ancyloceratids, the associating fauna consisting of *Chelonicer* spp., *Neosilesites* and *Valdedorsella* indicates a Lower Aptian age in both cases, and subsequent work by Förster (1975a) confirms this.

All the ancyloceratid fragments consist either of parts of the early whorls, parts of the uncoiled shafts and/or the crozier, and at the time of writing, no complete specimen has been found. Two different kinds of early whorls can be identified; one with a circular, the other with a subtrigonal whorl section, the latter type being commonest. The shaft and croziers, on the other hand are so varied that hardly two specimens are alike. In addition to differences in ornamentation, remarkable differences in size occur, Macro- and micro-conchs being present.

The early whorls with subtrigonal whorl section can be identified with *A. (Ad.) mozambiquense* Krenkel; those with circular whorl section are referred to a new species, *A. (Ad.) cooperi* sp. nov. Some types of shaft and crozier may tentatively be referred to the two species. However, due to the extreme variability, and the absence of any complete specimens for definite allocation, the shafts and croziers are referred in open nomenclature to *A. (Ad.)* gr. ex. *mozambiquense-cooperi*. Admittedly, this may be interpreted as vertical systematics *par excellence*, but in the authors' opinion this is preferable to the other alternatives—to ignore the material until such time as future collecting may hopefully yield a complete specimen, or to erect a number of species based on incomplete specimens as has so often been done in the past. Moreover, identification based on the shaft and crozier alone is impracticable as will be shown in the discussion below, for even unrelated groups of heteromorphs may have the same type of crozier.

#### *Ancyloceras (Adouliceras) mozambiquense* Krenkel, 1910

Figs 7, 8A–B, 9B, 10B, 11B, 12A, D

*Ancyloceras* sp. Kilian, 1902: 465.

*Ancyloceras fallauxi* Uhl. n. var. *mozambiquense* Krenkel, 1910: 153, pl. 17 (figs 2–3).

? *Ancyloceras fallauxi* Uhlig var. *mozambiquense*: Haughton & Boshoff, 1956: 14.

*Tropaeum mozambiquense*: Wachendorf, 1967: 292, pl. 34 (fig. 1). *Non* Da Silva 1962: 21, pl. 9 (figs 1–2), pl. 10 (fig. 1), pl. 11 (fig. 1), pl. 12 (fig. 1), pl. 13 (fig. 1), pl. 14 (fig. 1).

? *Tropaeum* cf. *hillsi*: Förster, 1975a: 151, pl. 2 (fig. 1), text-fig. 28.

*Australiceras mozambiquense*: Förster, 1975a: 155, pl. 3 (fig. 3), text-fig. 31.

*Holotype*

The specimen figured by Krenkel (1910, pl. 17 (figs 2-3)) reported to have been collected from near Delagoa Bay, Mozambique.

*Neotype*

SAM-PCM5349 (Fig. 7) from Lubemba, southern Mozambique. The holotype was destroyed by bombing during 1944.

*Material*

SAM-PCM5314, SAM-PCM5351, SAM-PCM5438 from Lubemba, southern Mozambique; SAS 54/45; SAS 54/41/4; SAS 54/45/2; BMNH C78883 and BMNH C78884 from locality 170, Mlambongwenya Creek, Zululand. Aptian I-II.

*Description*

Coiling is crioceratitid but very variable. On the most complete specimen, SAM-PCM5349 (Fig. 7), the inner whorl is not in contact with the outer. Some specimens, however, have a distinct dorsal impression of the ventral tubercles on the preceding whorl. The whorl section is typically subtrigonal to rectangular, higher than wide with a flattened but not impressed dorsum and slightly inflated flanks converging to a moderately rounded venter. In some specimens the dorsum is rounded and convex (Fig. 8A).

As can be seen from the impression of the inner whorl of specimen SAM-PCM5349 (Fig. 7), juvenile ornament consists of very fine, radial ribs which cross the dorsum with traces of duplication. The umbilical tubercles appear to be most prominent, and appear as low, rounded bosses, covering one to three ribs. The bosses probably indicate the former presence of long spines, with a basal septum. The lateral tubercles are smaller and more pointed. Ventral tubercles are not preserved, but judging by their impression on the dorsae of some of the larger whorls, were quite prominent and situated close to each other on either side of the siphonal line.

At larger diameters, ribbing becomes weaker and curves forward over the dorsum, although radial to slightly sinusoidal across the flanks. The ribs cross the venter without visible sign of interruption. Bifurcation of ribbing occurs at the umbilical edge, or on the dorsal third of the flanks. The diameter at which tuberculation disappears is very variable, the ventral and lateral tubercles disappearing first. At a whorl height of approximately 45 mm, the last umbilical tubercles are visible. There are about 11 to 13 ribs in a distance equal to the whorl height.

The suture is highly incised and dendritic. Unfortunately, however, none of the specimens is suitable for reproduction of the whole suture line.

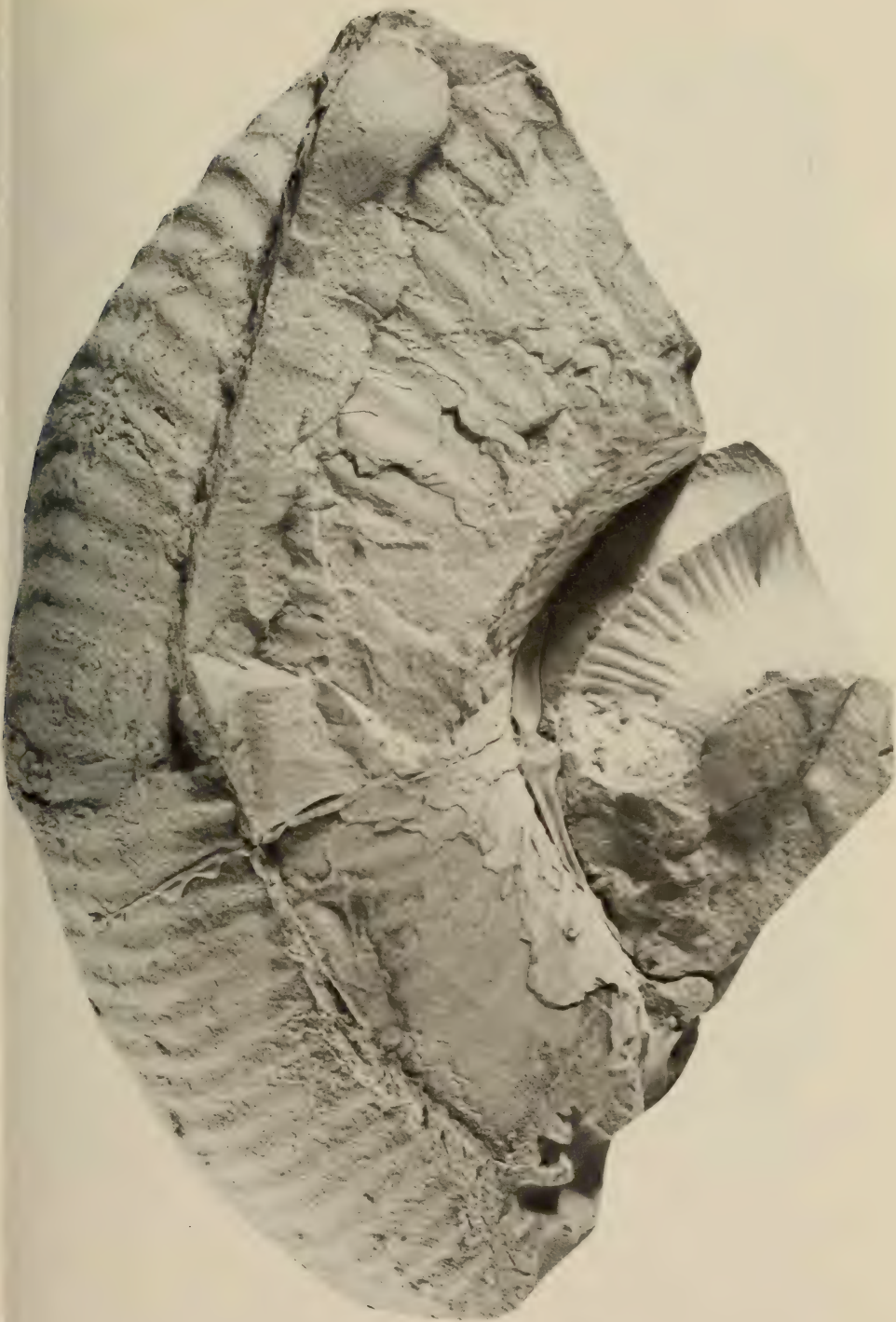


Fig. 7. *Ancyloceras* (*Adouliceras*) *mozambiquense* Krenkel, 1910. SAM-PCM5349, neotype from the Lower Aptian of Lubemba, Mozambique. Collected by M. R. Cooper.  $\times 1,3$ .





Fig. 8. *Ancyloceras (Adouliceras) mozambiquense* Krenkel, 1910. A. SAS 54/45. B. SAS 54/1. Both from the Lower Aptian, Aptian I-II of locality 170.  $\times 1$ .



Fig. 9. A. *Ancyloceras (Adouliceras) gr. ex mozambiquense-cooperi*. SAM-PCM5328, crozier from the Lower Aptian of Lubemba, Mozambique. Note the strong development of the umbilical and lateral tubercles.  $\times 0.85$ . B. *Ancyloceras (Adouliceras) mozambiquense* Krenkel, 1910. SAS 54/45/2 from locality 170, Zululand, Lower Aptian, Aptian I-II.  $\times 1$ .



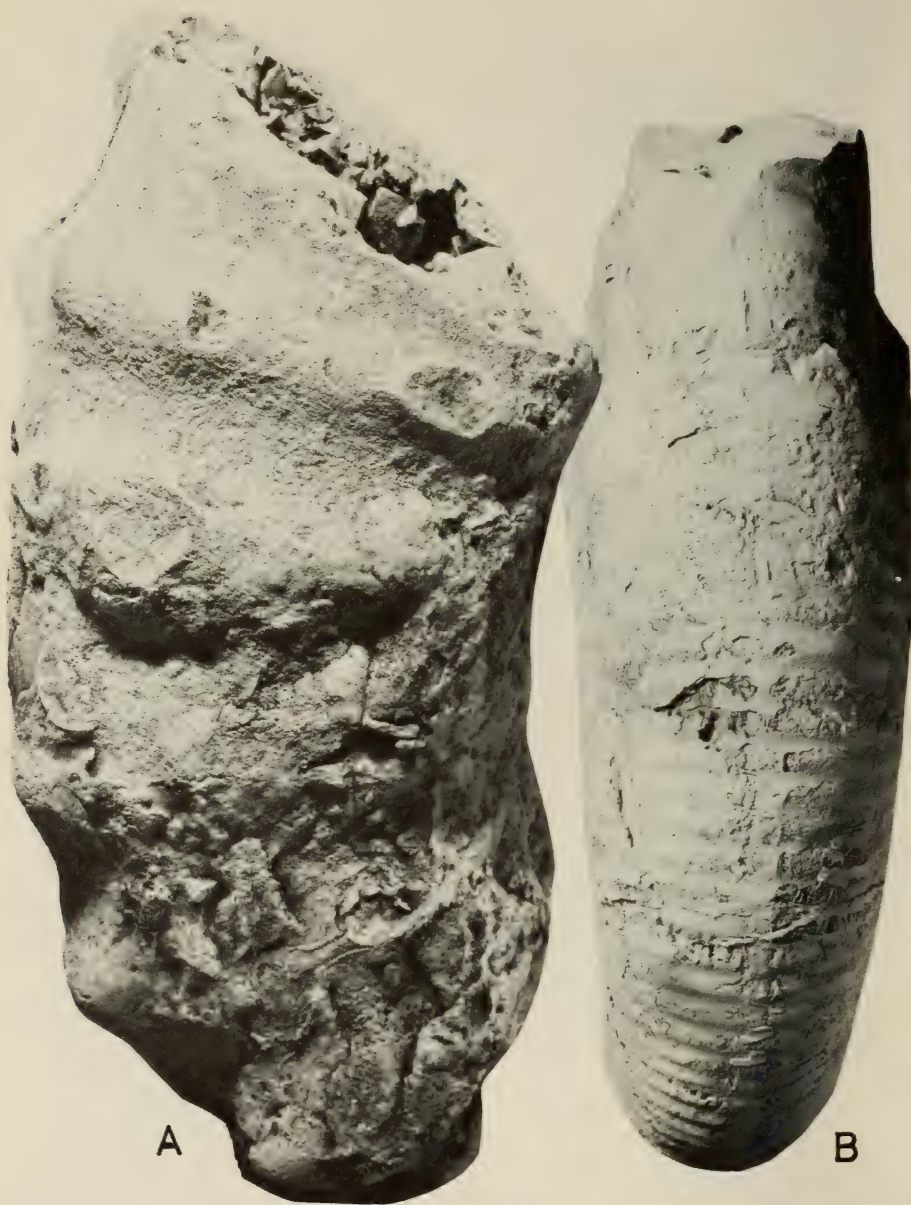
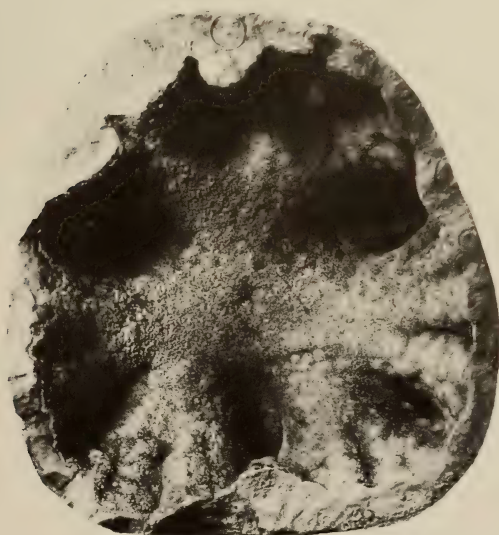


Fig. 10. A. *Australiceras*? sp. cf. '*Crioceras*' *sarasini* Favre, 1908, SAS H71D/18 from Nhlohlela pan, Mkuze Game Reserve, Zululand, Aptian III-IV.  $\times 1$ . B. *Ancyloceras* (*Adouliceras*) *mozambiquense*, SAS 54/45 from locality 170, Zululand, Aptian I-II.  $\times 1,2$ .





A



B

Fig. 11. A. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAS 54/45/3, crozier from locality 170, Zululand, Aptian I-II. Form 3 with only laterally developed tubercles in crozier.  $\times 0,54$ . B. *Ancyloceras* (*Adouliceras*) *mozambiquense* Krenkel, 1910. SAS 54/41/3 from locality 170, Zululand, Aptian I-II.  $\times 1,2$ .

*Dimensions*

<i>Specimen</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>
SAM-PCM5349	44	47	0,93
SAS 54/41/3	51,6	56,4	0,91

*Discussion*

It is difficult to understand how Krenkel's (1910: 153) original description of the species was so consistently misinterpreted by subsequent workers; Krenkel states of the unique holotype (destroyed during the Second World War):

‘. . . das aus dem Übergang des spiral eingerollten Teiles zum Schaft stammt. Die Innenseite zeigt keine Spur einer Berührung mit dem früheren Umgange.’

Da Silva's interpretation of Krenkel's species is unacceptable, and his *Tropaeum mozambiquense* was merely a catch-all for fragments of a variety of *Tropaeum*. The specimen which Da Silva (1962: 21, pl. 9, figs 1–2) described as corresponding to Krenkel's original, has a distinctly impressed dorsal zone, and this is a feature Krenkel explicitly stated to be absent. Förster (1975a) has recently described material from the same area in Mozambique, and he realized that most of Da Silva's specimens of '*Tropaeum mozambiquense*' were better referred to *Tropaeum subsimbirskense compressum* (Sinzow). Förster also noted the presence of three rows of tubercles on some of his material and concluded that Krenkel's species must be an australiceratid, with affinities with *A. rabenjanaharyi* Collignon and *A. ramososeptatum* (Anthula), again a departure from Krenkel's original concept.

Other finely ribbed species of *Tropaeum* bear a strong similarity to the non-tuberculate fragments of *A. (Ad.) mozambiquense*. On the basis of the present material, however, the ancyloceratid character of the species is firmly established.

*A. (Ad.) mozambiquense* is easily distinguished from other species of *A. (Adouliceras)* by the sub-triangular whorl section and by the relatively large planispirally coiled immature stage which is a departure from the normal *Adouliceras* pattern.

*Occurrence*

Lower Aptian, Aptian I–II of Zululand and southern Mozambique.

*Ancyloceras (Adouliceras) cooperi* sp. nov.

Figs 12B–C, 13A–C, 14A–C

*Holotype*

SAM-PCM5317 in the South African Museum, from Lubemba, southern Mozambique. Collected by M. Cooper. Aptian I–II.

*Derivation of name*

The species is named for Michael Cooper, of Wolfson College, Oxford, who collected the type material.

*Material*

Apart from the holotype; SAM-PCM5313, SAM-PCM5215, from Lubemba, and SAS 54/41/1 and SAS 54/41/2 from locality 170, Mlambo-gwenya, Zululand, Aptian I-II.

*Description*

Coiling is tight, resulting in a small planispirally coiled section. The whorls, however, are not impressed. The very early whorls are unknown, but at a diameter of *c.* 20 mm the section is already essentially circular, and only a little wider than high. The dorsum is slightly flattened, but with no trace of the impressed zone. Ornament initially consists of radial, single, broad, low ribs, each bearing three rows of low and rounded tubercles. The tubercles are of approximately equal size, and appear to be the bases of septate spines. The tuberculate ribs are separated by one or two narrow intermediaries. The latter are thin and separated by interspaces of equal width. They sweep backward over the umbilical wall, and are straight and radial to rursiradiate across the flanks and pass straight across the venter. On the dorsum, the ribs curve forward and show a notable tendency towards duplication. With increasing diameter the major ribs tend to become wider and the lateral and ventral tubercles disappear at a whorl breadth of around 23 mm. At this stage, ribs now arise in two's, three's and four's from the remaining, but weakened, umbilical tubercles. On the holotype, umbilical tubercles are still visible at a whorl breadth of 32 mm, but on another specimen, SAS 54/41/2 (Fig. 14), no sign of tubercles is visible at a whorl breadth of 21 mm. Two very slight constrictions are present on SAM-PCM5313.

*Dimensions*

<i>Specimen</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
SAM-PCM5317	89,2	37(41,4)	40,2(45)	0,92	33,5(37,5)

*Discussion*

The round whorl section clearly distinguishes *A. (Ad.) cooperi* from *A. (Ad.) mozambiquense*. Furthermore, the initial spire is much smaller in the former. The holotype bears a superficial resemblance to some of the species redescribed by Thomel (1964), e.g. *A. (Ad.) aff. collignoni* Sarkar, 1955 (Thomel 1964: 58, pl. 9 (fig. 1), text-fig. 7A), *A. (Ad.) kaliae* Sarkar 1955 (Thomel 1964: 57, pl. 10 (fig. 1), text-fig. 7B), and *A. (Ad.) adouli* Astier (Thomel 1964: 56, pl. 9 (fig. 2), text-fig. 7C) as far as the size of the planispirally coiled section is concerned. *A. (Ad.) adouli* has a whorl section similar to that of the present species, but lacks the regular tuberculation (see Thomel 1964: 58, fig. 7) and has



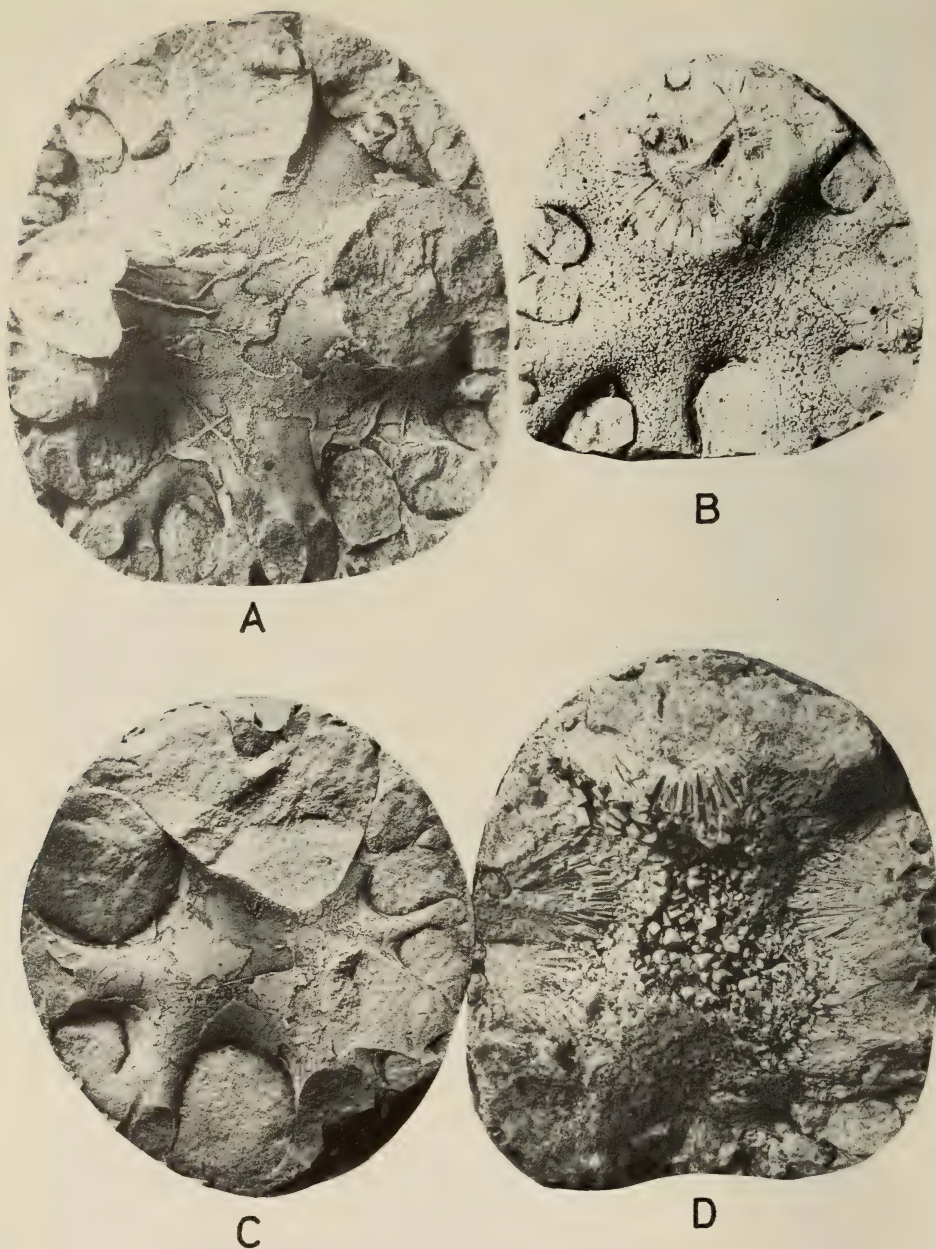


Fig. 12. A. *Ancyloceras (Adouliceras) mozambiquense* Krenkel, 1910. SAM-PCM5505 from Lubemba, Mozambique, Lower Aptian.  $\times 1,3$ . B. *Ancyloceras (Adouliceras) cooperi* sp. nov. SAM-PCM5215 from same locality and horizon as above.  $\times 1,4$ . C. *Ancyloceras (Adouliceras) cooperi* sp. nov. SAS 54/42/2 from locality 170, Zululand, Aptian I-II. Typical rounded form.  $\times 1,4$ . D. *Ancyloceras (Adouliceras) mozambiquense* Krenkel, 1910. SAM-PCM5351 from Mozambique, Lower Aptian.  $\times 1,3$ .

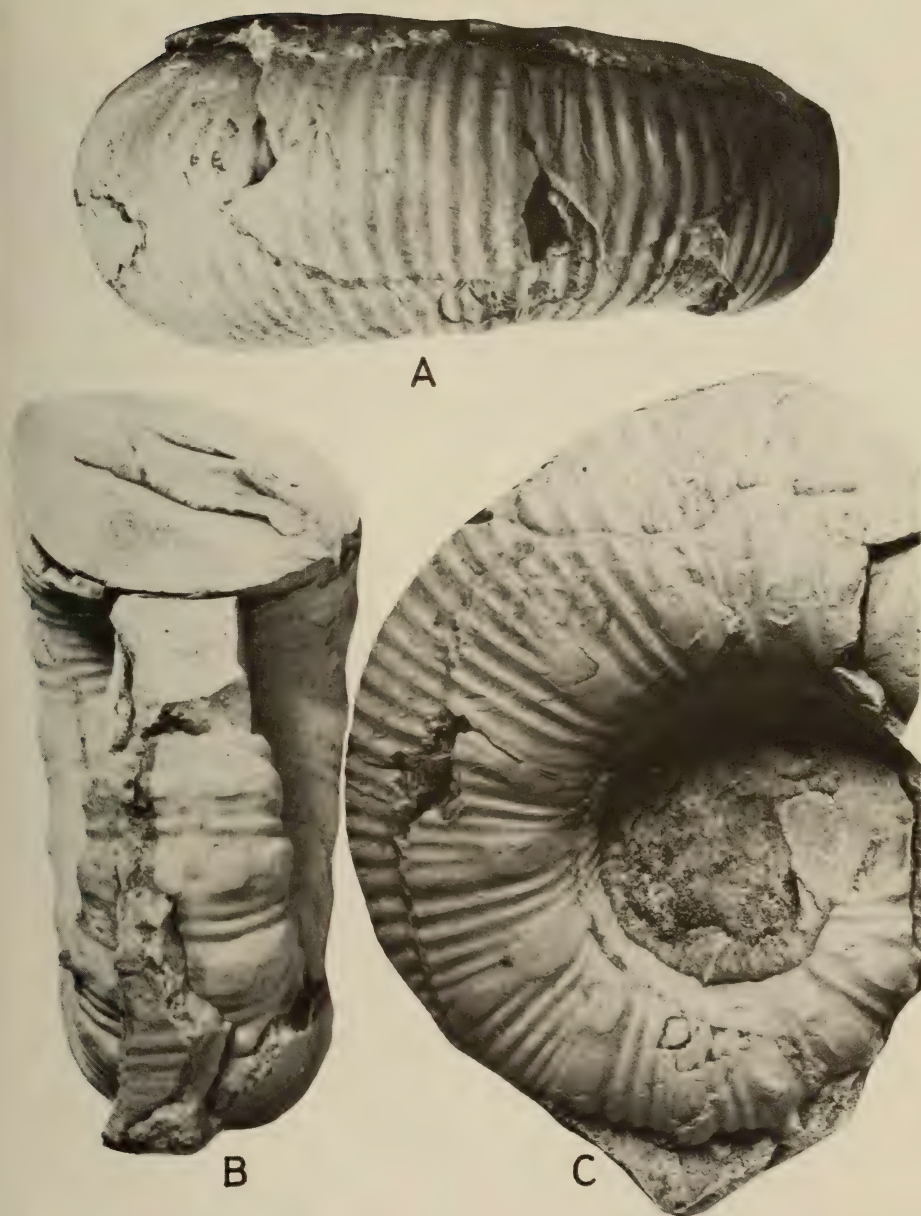


Fig. 13. A-C. *Ancyloceras* (*Adouliceras*) *cooperi* sp. nov. SAM-PCM5317, holotype from Lubemba, Mozambique, Lower Aptian.  $\times 1,05$ .



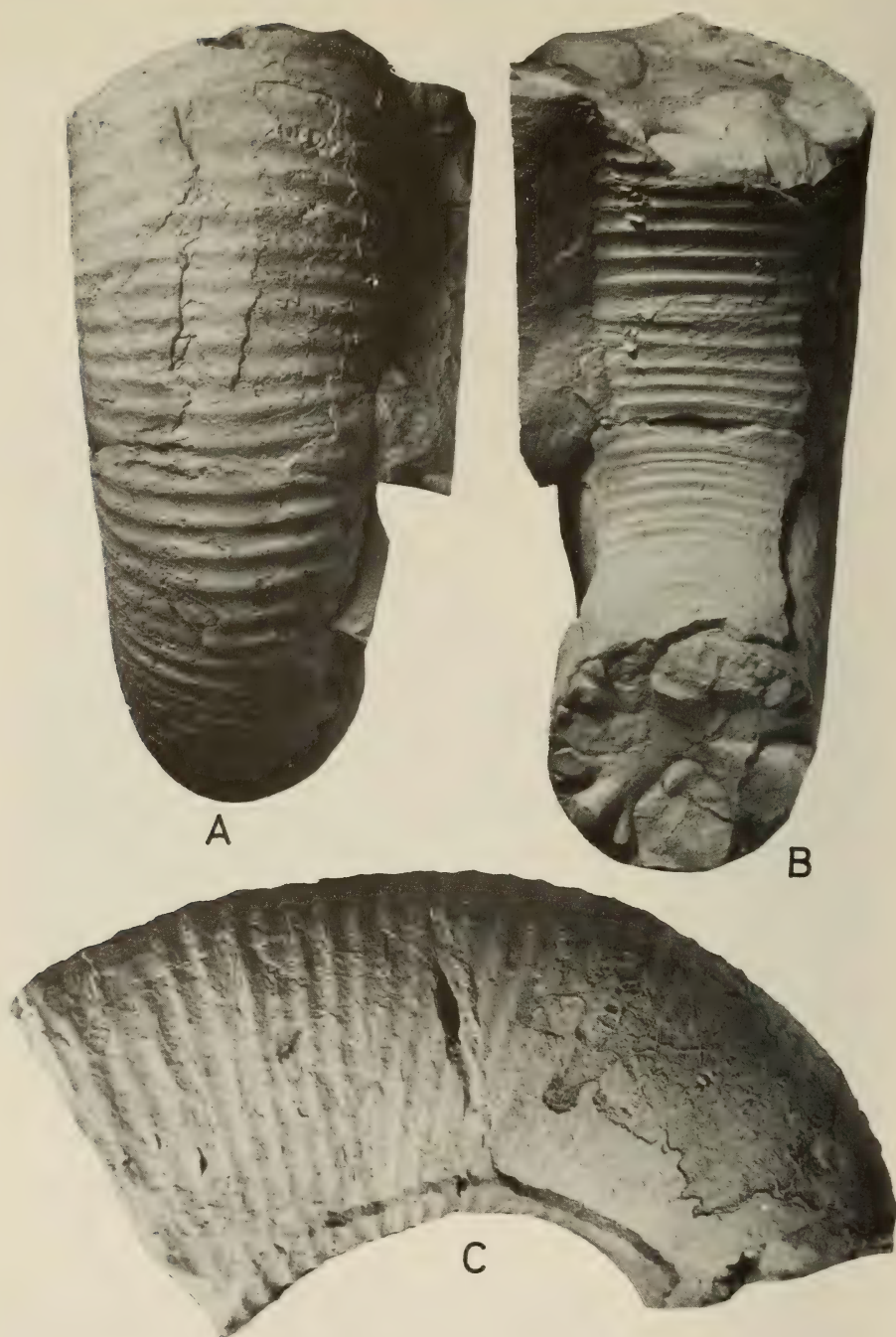


Fig. 14. A-C. *Ancyloceras* (*Adouliceras*) *cooperi* sp. nov. SAS 54/41/2 from locality 170, Zululand, Aptian I-II.  $\times 1$ .



numerous intermediary ribs. *A. (Ad.) kaliae* Sarkar from the Upper Barremian is very similar as far as ornamentation is concerned, but has an ovoid whorl section. *A. (Ad.)* aff. *collignoni* has irregular ornamentation.

#### Occurrence

Lower Aptian of Zululand and Mozambique.

*Ancyloceras (Ad.)* gr. ex. *mozambiquense-cooperi*

(Description of shafts and croziers)

#### Form 1

Figs 15, 16, 17, 18A, 19, 20A-B

#### Material

SAM-PCM5337, SAM-PCM5395, SAM-PCM5368, SAM-PCM5449, SAM-PCM5324, from Lubemba, southern Mozambique. BMNH C7884 from Locality 170, Zululand.

#### Description

The shaft is of variable length with a subtrigonal section, having a narrower venter than dorsum and weakly inflated flanks. Towards the crozier the dorsum becomes more flattened and the dorso-ventral width increases. In the bend of the crozier and on the descending limb the whorl section is dome-shaped with a flat dorsum and broadly rounded flanks and venter. There is no distinct inflation of the body chamber.

At the proximal end of the shaft, ornament consists of narrow, low, slightly prorsiradiate ribs only, separated by wider interspaces. Average rib density is about sixteen to eighteen per dorso-ventral diameter. On the distal half to third of the shaft, stronger ribs start appearing on the flanks, bearing umbilical and lateral tubercles. These ribs and the tubercles become progressively more prominent towards the bend in the crozier. At the bend the intermediaries become fainter and eventually disappear. In the bend itself, one or two of the major costae now acquire ventral tubercles and cross the venter with a forward curvature. At this stage the lateral tubercles are generally strongest. In the descending limb the ribs become narrower and increasingly flared, accompanied by loss of tuberculation. Three flared ribs are present in the most complete specimen.

The last septum occurs at a point coinciding approximately with the onset of major ribbing.

#### Dimensions

Specimen	SAM-PCM5324	SAM-PCM5368
Wb. at proximal end of shaft . . .	91	78
Wh. at proximal end of shaft . . .	105	87
Wb. in crozier . . . . .	117	99

Specimen	SAM-PCM5324	SAM-PCM5368
Wh. in crozier . . . . .	109	93
Wb. near aperture . . . . .	110	97
Wh. near aperture . . . . .	100	90
Width of crozier = venter of shaft to venter of descending limb . . . .	295	230

### Discussion

This is the most common form present, and it is likely that it belongs to the planispiral whorls identified as *A. (Ad.) mozambiquense*, which are also the most abundant, as is suggested by the subtrigonal whorl. Until more complete material becomes available to substantiate or discredit this assumption, it is considered advisable to refer the shafts and croziers in open nomenclature to *A. (Ad.)* gr. ex. *mozambiquense-cooperi*.

A number of shafts and croziers from various unrelated species with quite distinct early whorls are virtually identical to, or impossible to distinguish from, the group of specimens available. These include *A. (Ad.?) durrelli* Anderson (1938: 210, pl. 65 (figs 1-2), pl. 68 (fig. 1)), *Ancyloceras matheronianum* d'Orbigny in Drushchitz & Kudryavtsev (1960, pl. 34 (fig. 2)), *Ancyloceras urbani* Neumayr & Uhlig, 1881, and *Ancyloceras rochi* Dimitrova (the latter two in Dimitrova 1967, pls 23, 24 respectively), and it is apparent that species based on croziers and shafts are of little value in at least some ancyloceratid genera.

### Form 2

#### Fig. 21B

### Description and discussion

Crozier SAS 54/45/5 is virtually identical to the previous form as far as ornamentation is concerned, but is only half the size. These differences probably reflect sexual dimorphism, although this has not been widely recognized in ancyloceratids.

### Dimensions

Wb. at proximal end of shaft . . .	54
Wh. at proximal end of shaft . . .	66
Wb. in crozier . . . . .	66
Wh. in crozier . . . . .	—
Wb. near aperture . . . . .	71
Wh. near aperture . . . . .	67
Width of crozier . . . . .	180

### Form 3

#### Figs 11A, 23

### Description and discussion

Crozier SAS 54/45/3 has only one lateral row of irregularly developed tubercles and does not develop flared ribbing immediately before the aperture.

*Dimensions*

Wb. at proximal end of shaft . . . . .	—
Wh. at proximal end of shaft . . . . .	78
Wb. in crozier . . . . .	c. 91
Wh. in crozier . . . . .	81
Wb. at aperture . . . . .	92
Wh. at aperture . . . . .	86
Width of crozier . . . . .	215



Fig. 15. *Ancyloceras* (*Adoulterias*) gr. ex *mozambiquense-cooperi*. SAM-PCM5324, crozier from Lubemba, Mozambique. Lower Aptian. Most common form, Form 1.  $\times 0,48$ .





Fig. 16. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM-PCM5324, ventral view of crozier from Lubemba, Mozambique, Lower Aptian. Most common form, Form 1.  $\times 0,57$ .

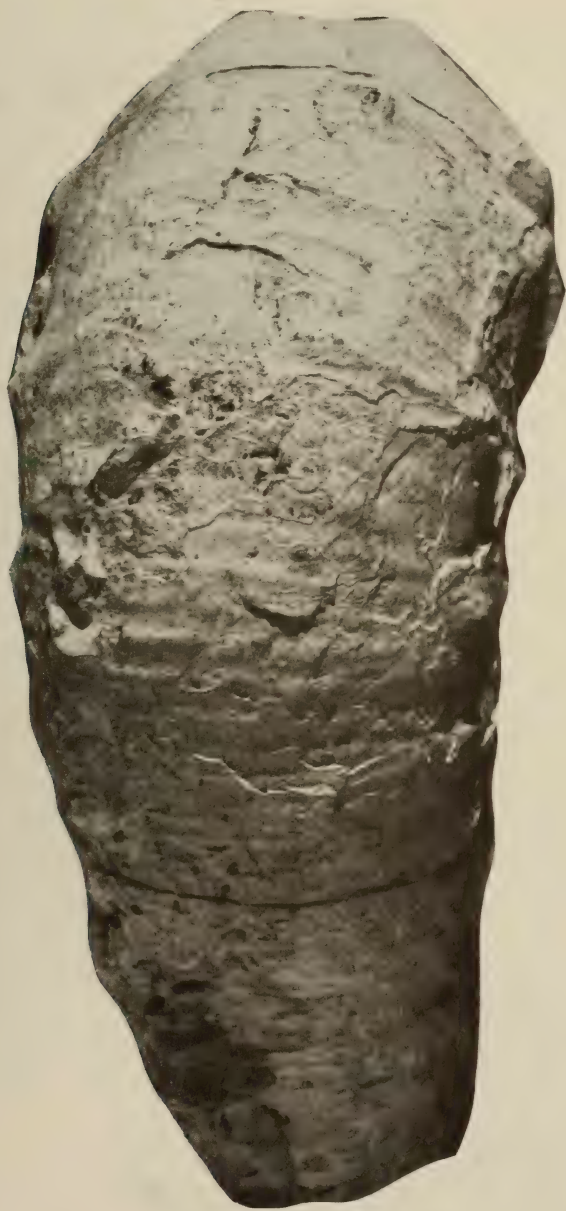


Fig. 17. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM-PCM5368, ventral view of crozier from Lubemba, Mozambique, Lower Aptian. Most common form, Form 1.  $\times 0,67$ .



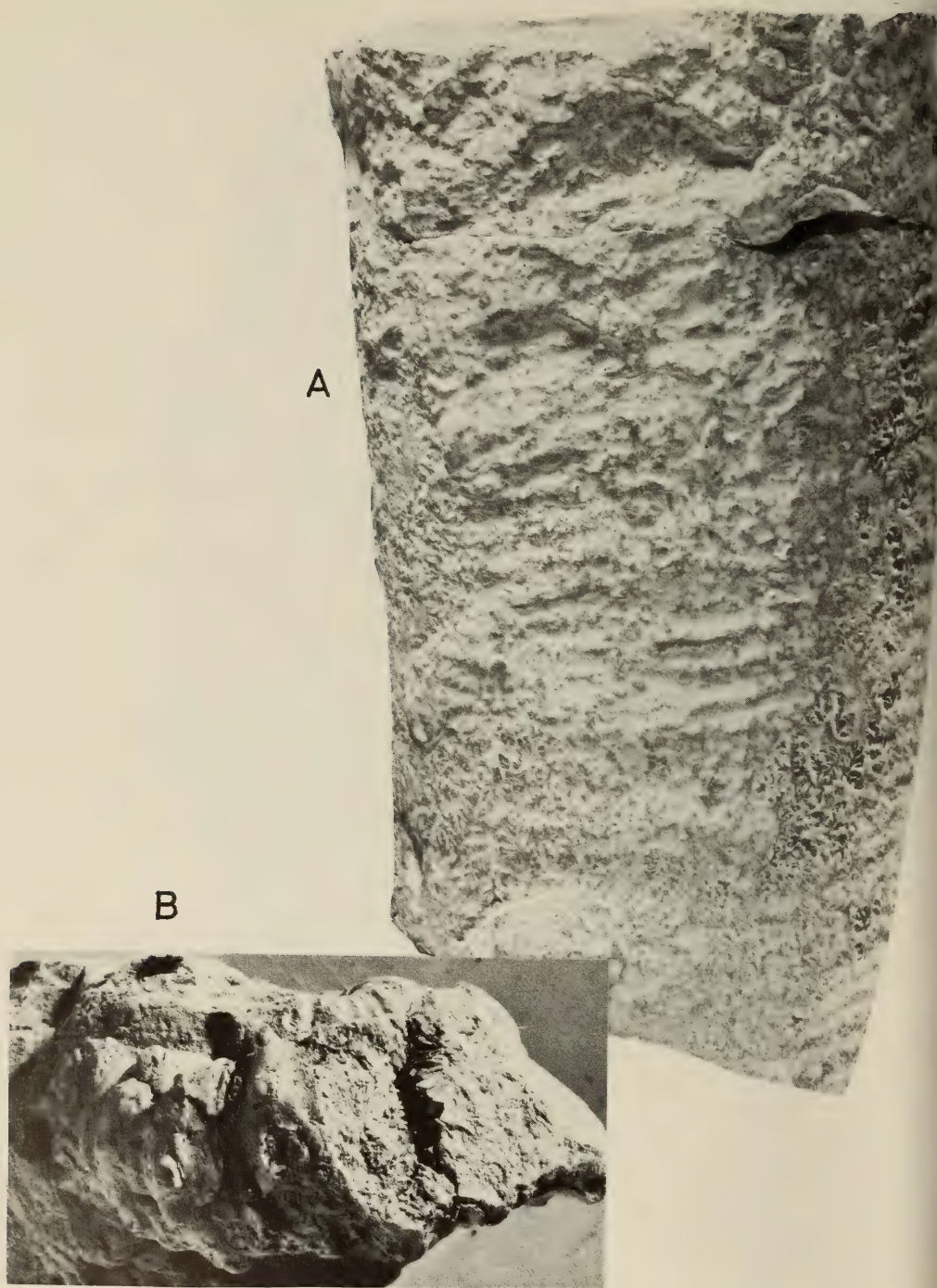


Fig. 18. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM-PCM5449, lateral view of shaft from Lubemba, Mozambique, Lower Aptian. Most common form, Form 1.  $\times 0,77$ . B. *Ancyloceras* (*Ancyloceras*?) sp. indet. SAS B11 from locality 170, Zululand, Aptian I.  $\times 1,55$ .





Fig. 19. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM-PCM5337 from Lubemba, Mozambique, Lower Aptian. Most complete shaft of common form, Form 1.  $\times 0,68$ .



Fig. 20. A-B. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. BMNH C78884 from locality 170, Zululand, Aptian I-II. Specimen with finer ribbing than previous examples.  $\times 0,67$ .

#### *Form 4*

#### Fig. 21A

#### *Description and discussion*

Crozier SAS 54/45/6 completely lacks major ribbing on the ascending shaft. This crozier may be compared with *A. (Ad.) ewaldi* Dames (1880: 690, pl. 25, pl. 26 (fig. 1)). The latter species, however, has stronger and more rounded ribbing on the shaft. This specimen is crushed, hence no measurements are given.

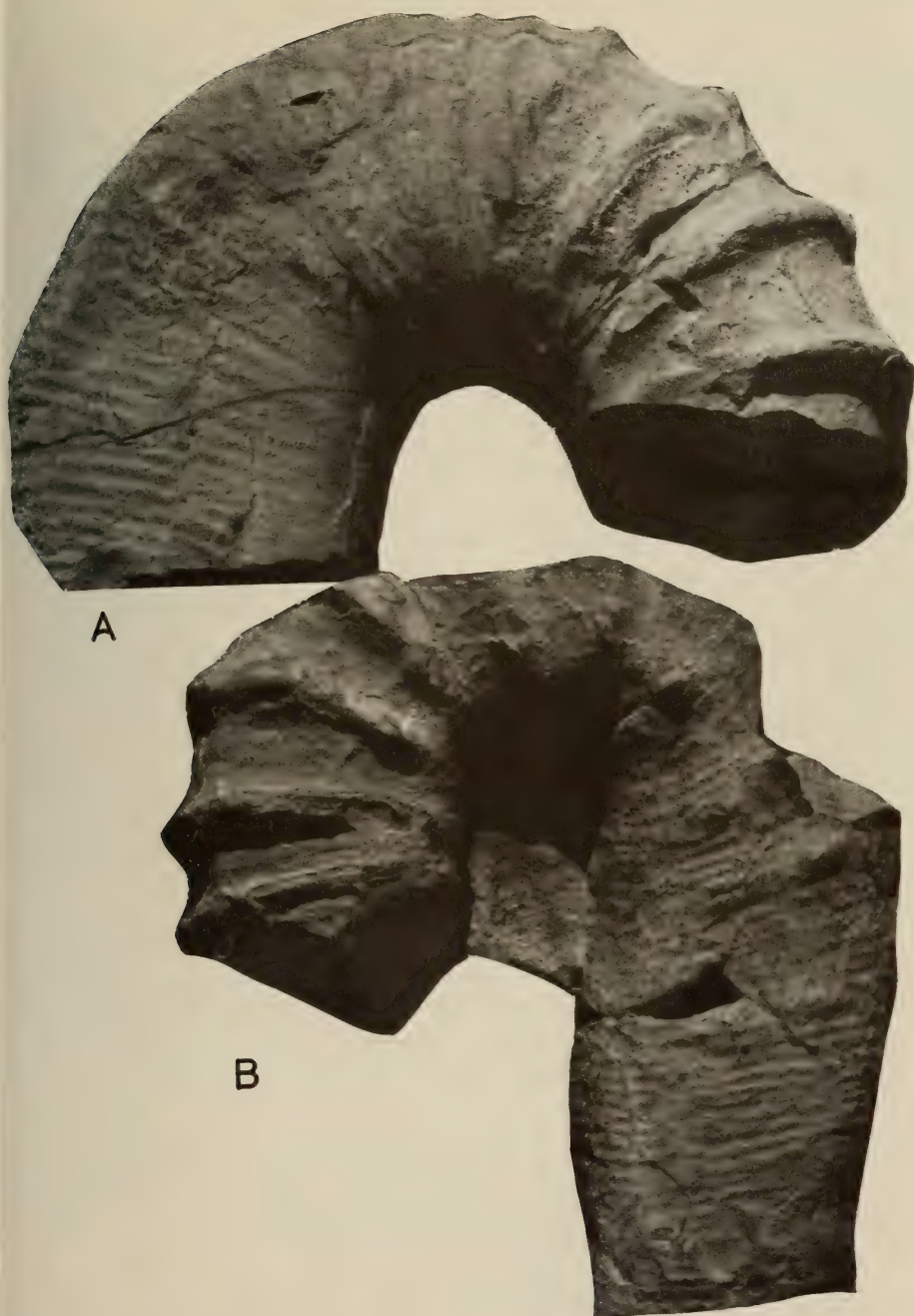


Fig. 21. A-B. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. A. SAS 54/45/6 from locality 170, Zululand, Aptian I-II. Form 4.  $\times 0,57$ . B. SAS 54/45/5 from same locality and horizon as above. Form 2.  $\times 0,53$ .



*Form 5*

## Fig. 22

*Description and discussion*

Crozier SAS 54/45/4 is a micromorph with an ovoid whorl section on the shaft and with plain, simple ribbing throughout, apart from a smooth zone on the descending shaft and a slightly flared rib just before the aperture. A few paired ribs are more prominent than the others.

The rounded whorl section may indicate that this type of crozier may belong to the inner whorls referred to *A. (Ad.) cooperi* sp. nov. The absence of major costae on the crozier is reminiscent of that of *Colchidites colchicus* Djanélidzé (1926, pl. 1 (fig. 1)). The smooth part of the descending limb (which may be a malformation) is reminiscent of Anderson's (1938) genus *Shastoceras*. The body chamber of *Shastoceras*, however, is inflated and internal moulds are reportedly smooth.

*Dimensions*

Wb. at proximal end of shaft . . .	54
Wh. at proximal end of shaft . . .	57
Wb. in crozier . . . . .	77
Wh. in crozier . . . . .	c. 66
Wb. at aperture . . . . .	80
Wh. at aperture . . . . .	73
Width of crozier . . . . .	175
Length of shaft to bend in crozier .	170

*Form 6*

## Figs 9A, 24

*Description and discussion*

A single specimen, SAM-PCM5328 represents that part of a specimen at the point where the shaft begins curving into a crozier. Three sets of major ribs are present, separated by two to three low, rounded ribs. On the first major rib three rows of tubercles are present, of which the lateral one is best developed. At the distal end, however, only umbilical and lateral tubercles remain, but the lateral tubercle is enormous.

Viewed laterally there is resemblance to Murphy's *Ancyloceras thomeli* (1975: 24, pl. 3 (figs 1, 5), pl. 11 (figs 1-2)). In the Californian species, however, the ventral row of tubercles only appears towards the bend in the crozier, whereas the reverse holds true for the Zululand specimen.

Genus *Lithancylus* Casey, 1960*Type species*

*Hamites grandis* J. de C. Sowerby, 1828 from the Lower Aptian of southern England by original designation of Casey (1960: 16).

*Diagnosis*

Coiling probably ancyloceratid, with a long, curved or straight shaft, ending in a recurved hook. Section of shaft circular to oval, sub-octagonal on crozier. Ornament consists of low, rounded oblique ribs on the shaft; towards the crozier trituberculate ribs occur.



Fig. 22. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAS 54/45/4 from locality 170, Zululand, Aptian I-II. Form 5.  $\times 0,59$ .



Fig. 23. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAS 54/45/3 from locality 170, Zululand, Aptian I-II. Form 3.  $\times 0,79$ .





Fig. 24. *Ancyloceras* (*Adouliceras*) gr. ex *mozambiquense-cooperi*. SAM-PCM5328 from Lubemba, Mozambique, Lower Aptian. Form 6.  $\times 0.8$ .

### Discussion

This is a relatively rare genus, characterized by the long, plainly ribbed shaft ending in a crozier with trituberculate ribs. The presence of an initial planispirally coiled part has yet to be demonstrated.

Apart from the type species, the genus is represented by *L. fustis* Casey (1961: 75, pl. 21 (fig. 4a–d)) from the Lower Aptian of southern England, *L. tirolensis* Casey (1961: 74, text-fig. 29) from the Upper Barremian of Puez Alp, Tyrol, *L. mirabilis* Anderson (1938: 220, pl. 78 (figs 1, 2a, 3)), *L. nauplius* Anderson (1938: 221, pl. 66 (fig. 2–2a)), *L. neleus* Anderson (1938: 221, pl. 59 (fig. 2–2a)), and *L. cyclopius* Anderson (1938: 221, pl. 58 (fig. 3), pl. 66 (fig. 3–3a)), all from the Horsetown Beds of California, and probably of Barremian to Aptian age. *L. australe* Day (1967: 19, pl. 2 (figs 1–5), text-fig. 2) is from the Aptian of the Eromanga Basin of Queensland, Australia, and *L. guanacoensis*

Leanza (1970: 204, fig. III, 1-4) is reported from Patagonia. Thomson (1974: 15, pl. 2 (fig. 1) tentatively referred a specimen from Alexander Island (Falkland Island Dependencies) to *Lithancylus*. Reference of the Bulgarian specimen of *Ancyloceras elephas* Anderson, 1938 to *Lithancylus* by Dimitrova (1967: 61, pl. 29 (fig. 1)) is questionable. The Bulgarian specimen shows an inflated body chamber which is a characteristic of *Ancyloceras* (*Adouliceras*) rather than *Lithancylus*.

Differentiation of species is based mainly on the whorl section of the shaft and the density of ribbing thereupon.

#### Occurrence

Upper Barremian and Lower Aptian of England, Tyrol, California, Falkland Island Dependencies?, Patagonia, Mozambique and Australia.

#### *Lithancylus* sp.

Figs 25A-B, 83A, 84A-C

#### Material

SAM-PCM5436 from Lubemba, southern Mozambique.

#### Description

A straight, septate piece of shaft is probably referable to this genus. At the proximal end the whorl section is subtrigonal, with a broadly rounded dorsum and little-inflated flanks converging to a narrower, rounded venter. At the distal end the whorl section is virtually equidimensional, and octagonal. Ornament at the proximal end consists of low, rounded prorsiradiate ribs, separated by interspaces wider than themselves. It appears as if the ribs are weaker on the dorsum than on the flanks. At the distal end, three stronger trituberculate ribs occur, separated by two intermediary ribs. One pair of tubercles is situated ventrally, the other on the ventral third of the flanks and the third, which is smallest and virtually imperceptible, on the dorsal third of the flanks.

The suture line is very incised with trifid L, U and I lobes and bifid saddles.

#### Dimensions

Wb.	47,2	
		(at distal end)
Wh.	52,9.	

#### Discussion

This specimen corresponds approximately to Casey's *Lithancylus grandis* (Sowerby) specimen figured in his plate 20, fig. 1b, where ornament on the shaft changes from normal to trituberculate ribbing. *L. grandis*, however, has an almost circular whorl section on the shaft and is not conspecific. *L. fustis* has a depressed whorl section; *L. neleus* (Anderson), *L. mirabilis* (Anderson) and *L. australe* Day have ovoid whorl sections. *L. cyclopius* (Anderson) has a subtrigonal section as the present specimen, but finer ribbing, as has *L. tirolensis* Casey.

Thomson's (1974) *Lithancylus* sp. is poorly preserved, but appears to have finer ribbing at the proximal end.

Associated shafts of *Ancyloceras* (*Adouliceras*) spp. are all more massive and have finer ribbing.

*Occurrence*

Lower Aptian of southern Mozambique.

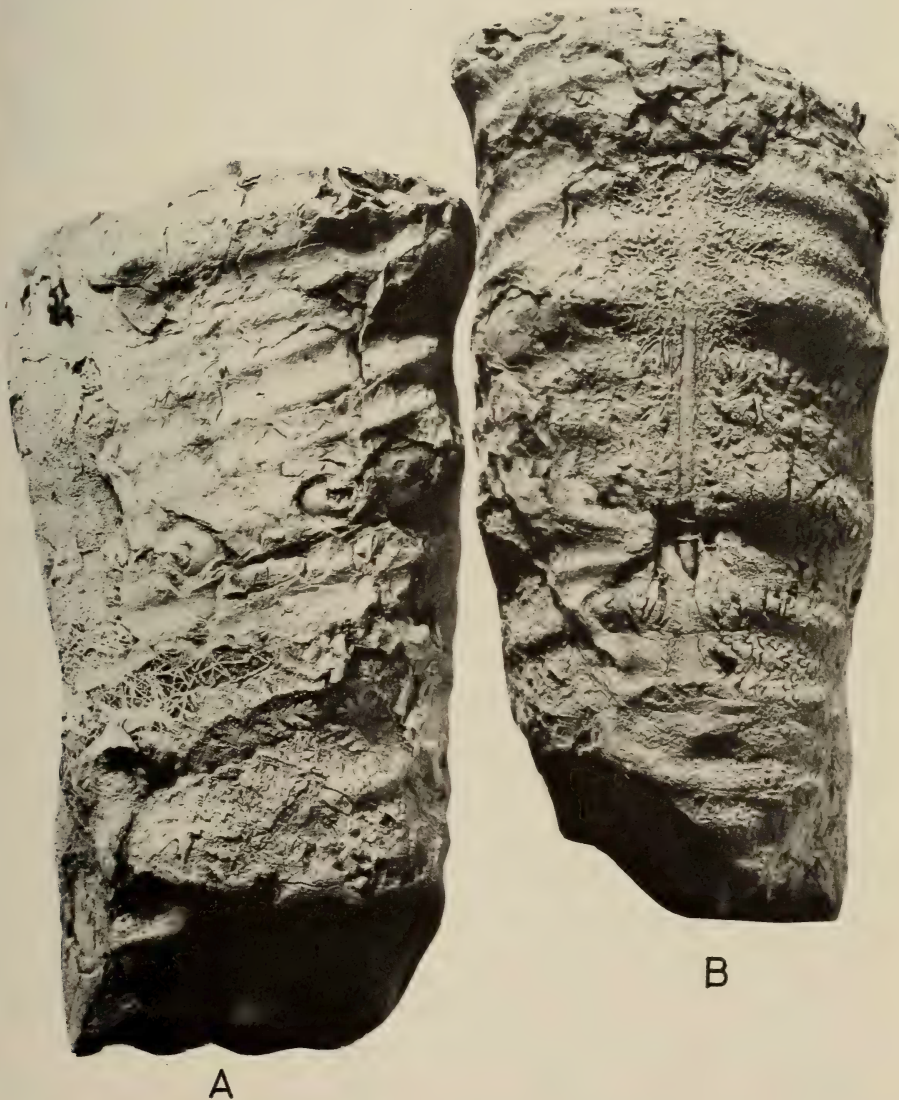


Fig. 25. *Lithancylus* sp. SAM-PCM5436 from Lubemba, Mozambique, Lower Aptian.  $\times 1,2$ .



Genus *Tropaeum* J. de C. Sowerby, 1837*Type species*

*Tropaeum bowerbanki* J. de C. Sowerby, 1837 from the Lower Aptian of England, by monotypy.

*Diagnosis*

Generally large; coiling predominantly crioceratitid, but in early species the body chamber may be distinctly uncoiled, giving rise to ancyloceratid or to aspinoceratid forms. Ornament on phragmocone consists of plain ribbing with occasional umbilical or ventral tubercles in early or late stages. On the body chamber a rapid change in ornament may take place, with the development of heavy, distantly spaced ribs. Aperture may be contracted. Dorsum ornamented by forward directed striae only.

*Discussion*

For details on the somewhat unusual manner in which the genus was introduced, and the accompanying nomenclatorial implications, see Casey (1960: 24), who also provides the most complete discussion of the genus. Additional information is provided by Day (1974: 5) who emended the diagnosis to accommodate loosely coiled forms and those in which no abrupt change in ornament takes place on the body chamber.

The best documented occurrences of *Tropaeum* are in England, the Caucasus and transcaspien regions of the U.S.S.R., and Australia. Recent descriptions of the English and Australian faunas are available, but for descriptions of the Russian species we are still heavily dependent on the older works of Sinzow (1872, 1905).

Together with the puzosiids, e.g. *P. seppenradensis* (Landois) and baculitids, e.g. *Baculites rex* Anderson and *Eubaculites latecarinatus* Brunn-schweiler (unpublished data on Zululand specimens), *Tropaeum* are amongst the largest Cretaceous ammonites. Förster 1975a: 153) recently described a specimen of *Tropaeum subsimbirskense compressum* (Sinzow) from the Aptian of Mozambique with a diameter of over 900 mm. *Tropaeum imperator* Howchin & Whitehouse (1928: 487, figs 144–145) is reported to be over 770 mm in diameter (Casey 1960: 41). A body chamber fragment from Zululand to be described below measures c. 730 mm, and a virtually complete specimen 700 mm. The large size, and loose crioceratitid or even ancyloceratitid coiling of the genus suggests that *Tropaeum* may have been a poor swimmer and led a rather sluggish life.

With the exception of some species which may possess tubercles in the early or late stages, e.g. *Tropaeum imperator* Howchin & Whitehouse, the genus is easily distinguished from the other ancyloceratids by the general lack of tubercles.

Within the genus, three species groups, based on the coiling of the body chamber, may be recognized:

- (i) *Tropaeum* gr. ex. *hillsi* J. de C. Sowerby
- (ii) *Tropaeum* gr. ex. *bowerbanki* J. de C. Sowerby
- (iii) *Tropaeum* gr. ex. *subarcticum* Casey

In each of these groups, successive species show parallel evolution of the outer whorls and body chamber with ancyloceratid, aspinoceratid and crioceratitid coiling respectively. This is a parallel development to that encountered in *Australiceras*, to be discussed below, and, as demonstrated by Casey (1960: 20, text-fig. 5), is one of the several examples of recoiling seen in ancyloceratids.

Specific differentiation amongst *Tropaeum* species is rather unsatisfactory, but is based primarily on the coiling of the outer whorls and body chamber, whorl section and ornamentation of the adult body chamber. Specific identification of fragments is usually virtually impossible. Species to be referred and possibly belonging to *Tropaeum* are as follows:

1. *Tropaeum?* *aegoceras* (von Koenen) (1902: 328, pl. 36 (fig. 1a-c)).
2. *Tropaeum arcticum* (Stolley) (1912: 16, pl. 2 (fig. 1)).
3. *Tropaeum australe* (Moore) (1870: 257, pl. 15 (fig. 3)).
4. *Tropaeum benstedti* Casey (1960: 37, pl. 3 (fig. 3), text-fig. 11g).
5. *Tropaeum bowerbanki* J. de C. Sowerby (1837: 535).
6. *Tropaeum bowerbanki* Sow. var. *densistriatum* Casey (1960: 30, pl. 6 (fig. 1)).
7. *Tropaeum caseyi* Collignon (1962: 18, pl. 222 (fig. 965)).
8. *Tropaeum drewi* Casey (1960: 35, pl. 8 (figs 1-2)).
9. *Tropaeum hillsi* (J. de C. Sowerby) (1836: 128).
10. *Tropaeum imperator* Howchin & Whitehouse (1928: 487, figs 144-145).
11. *Tropaeum keepingi* Casey (1960: 41, text-figs 11e, 13).
12. *Tropaeum?* *lamprum* (Etheridge Jun.) (1909: 157, pl. 48 (figs 1-2)).  
(According to Day (1974: 12) the holotype of this species is distinctly trituberculate and thus an *Australiceras*.)
13. *Tropaeum leptum* (Etheridge Jun.) (1909: 143, pl. 30 (figs 1-3), pl. 34 (fig. 2)).
14. *Tropaeum?* *multicingulatum* (Von Koenen) (1902: 314, pl. 34 (fig. 2)).
15. *Tropaeum rossicum* Casey (1960: 25).
16. *Tropaeum simbirskense* (Sinzow) (1872: 33, pl. 5 (figs 2-5), pl. 6 (figs 1-4)).
17. *Tropaeum subarcticum* Casey (1960: 40, pl. 8 (fig. 3a-c), pl. 10 (fig. 1), text-figs 11d, 12).
18. *Tropaeum subsibirskense subsibirskense* (Sinzow) (1905: 320, pl. 22 (figs 3-5)).
19. *Tropaeum subsibirskense compressum* (Sinzow) (1905: 230, pl. 22 (figs 1-2)).
20. *Tropaeum undatum* Whitehouse (1926: 215).

### Occurrence

*Tropaeum* occurs in the Aptian of England, northern Germany, the caucasian and transcaspian regions of the U.S.S.R., Bulgaria, Spitzbergen, eastern Greenland, arctic Canada, California, Japan, Patagonia, Falkland Island Dependencies?, Australia, Madagascar, Mozambique and Zululand.

*Tropaeum* sp. aff. *subsimbirskense subsimbirskense* (Sinzow, 1905)

Figs 26, 27A–B

Compare:

*Crioceras subsimeirskense* (sic) var. *inflata* Sinzow, 1905: 320, 330, pl. 22 (figs 3–5).

? *Tropaeum subsimbirskense compressa*: Dimitrova, 1967: 63, pl. 12 (fig. 1).

#### Material

SAS EM 109 from Manyola Drift, northern Zululand (26°50'20"S 32°13'5"E).

#### Description

Coiling is very involute, with an umbilical diameter of 33,5 per cent. The whorl section is rounded subtriangular with a flat dorsum, sharp umbilical edge and very little-inflated flanks converging to a sharp, narrow venter. The body chamber remains in contact with the phragmocone.

Ornament on the phragmocone consists of fine, sinusoidal ribbing. The ribs are faint on the dorsum and curve broadly forward. At the umbilical edge they curve sharply backward, forming a slight elevation, and then cross the flanks in sinusoidal fashion. Bifurcations and intercalations occur quite frequently at midflank or ventral thereof. On the nucleus, there are approximately seventy ribs per whorl. Towards the body chamber ornament gradually becomes coarser. On the earliest part of the body chamber virtually every rib bifurcates on the ventral quarter of the flanks, thus forming loops over the venter. Thereafter intercalated ribs arising on the ventral half of the body chamber replace the bifurcating ribs. On the last part of the body chamber, only strong, relatively high-crested ribs are present, separated by much wider interspaces. Each of these ribs has a prominent forward curvature over the venter. The suture line is very incised, with a huge lateral lobe.

#### Dimensions

Specimen	D	Wb	Wh	Wb/Wh	U
SAS EM 109	305	95(31,6)	112(37,2)	0,85	102(33,5)

#### Discussion

Casey (1960: 39 footnote) remarked that one of Sinzow's varietal names, *inflata* or *compressa* was superfluous, and subsequently regarded the variety *inflata* as representing *T. subsimbirskense* s.s. with Sinzow's (1905, pl. 22 (figs 4–5)) specimen as lectotype.

It should be pointed out here that the original spelling in the Russian text (Sinzow 1905: 320) is *subsimeirskense*, and *subsimbirskense* in the German résumé. The species is named after the Russian district of Simbirsk, and the name in the Russian text is obviously a typographical error. The valid name is thus *subsimbirskense*.



*T. subsimbirskense subsimbirskense* differs from the subspecies *compressum* in having a more inflated and depressed whorl section and a smaller umbilical diameter. Ribbing on the nominal subspecies also appears to be more sinusoidal when compared to the rursiradiate to rectiradiate ribbing of the subspecies *compressum*.

Dimitrova's (1967: 63, pl. 12 (fig. 1)) specimen is more suitably placed in the nominal subspecies rather than in *T. subsimbirskense compressum*.



Fig. 26. *Tropaeum* aff. *subsimbirskense subsimbirskense* (Sinzow, 1905). SAS EM 109 from Manyola Drift, Zululand, Aptian III.  $\times 0,3$ .



Fig. 27. A-B. *Tropaeum* aff. *subsimbirskense subsimbirskense* (Sinzow, 1905). SAS EM109 from Manyola Drift, Zululand, Aptian III.  $\times 0,34$  and  $0,55$  respectively.

The Zululand specimen differs from *T. subsimbirskense subsimbirskense* mainly in not being quite as inflated and in lacking the strong major costae with intermediaries on the body chamber, and is hence referred to the Russian species in open nomenclature. The umbilical diameter of the Zululand specimen is intermediate between that of Sinzow's two figured specimens.

In the lack of a sudden change of ornament on the body chamber, the present species is similar to the Australian *Tropaeum undatum* Whitehouse 1926 (see Day 1974: 6, pl. 3 (fig. 2a-b)). The latter species has, however, a subquadrate whorl section and much stronger ribbing.

#### Occurrence

Aptian III of Zululand.

#### *Tropaeum subsimbirskense compressum* (Sinzow, 1905)

Figs 28, 29A-B, 37

*Crioceras subsimeirskense* var. *compressa* Sinzow, 1905: 320, pl. 22 (figs 1-2) (error).

*Tropaeum mozambiquense*: Da Silva, 1962: 24, pl. 9 (figs 1-2), pl. 12, *non* pl. 10, pl. 11, pls 13-14.

? *Australiceras* cf. *gigas*: Wachendorf 1967: 283 pl. 34 (fig. 4).

? *Ammonitoceras tovilense*: Wachendorf, 1967: 282, pl. 36 (fig. 1).

*Tropaeum subsimbirskense compressum*: Förster, 1975a: 152, pl. 2 (figs 3-6), text-fig. 29.

*Non* Dimitrova, 1967: 63, pl. 12 (fig. 1).

#### Lectotype

Sinzow's (1905, pl. 22 (fig. 1)) specimen is herein designated lectotype. So far as can be determined, Sinzow did not designate a holotype. Dimitrova (1967: 63) stated that Sinzow's plate 22, figure 1 specimen is the type, but this cannot be taken as a lectotype designation.

#### Material

SAS EM 110 from Manyola Drift, Zululand. Aptian III.

#### Description

Coiling is closely crioceratitid with no sign of uncoiling of the body chamber. The innermost whorls, up to a diameter of 75 mm, are not preserved. At a diameter of 160 mm the whorl section is subtriangular with a flat to concave dorsum, a sharp umbilical edge, very little-inflated flanks and a narrow venter. Apart from the fact that the whorl height increases more rapidly than the whorl breadth, the whorl section remains basically subtriangular up to the body chamber. On the body chamber the umbilical wall becomes more rounded, the umbilical edge less acute and the flanks more inflated. The whorl section becomes subrectangular at this stage.

On the inner whorls, ornament consists of single, low, rounded rursiradiate to radial ribs separated by interspaces of the same width. At a diameter of approximately 300 mm occasional stronger ribs occur, separated by three to five





Fig. 28. *Tropaeum subsimbirskense compressum* (Sinzow, 1905). SAS EM110 from Manyola Drift, Zululand, Aptian III.  $\times 0,25$ .

normal ribs which may bi- or trifurcate at the umbilical edge. Towards the end of the phragmocone the major ribs become stronger. The beginning of the body chamber is marked by a very strong, low broad rib. From here onward, as far as the aperture, ornament consists solely of ten widely spaced, initially low, broad ribs; the intercalatories having disappeared completely. Towards the aperture, the last four or five major ribs become progressively flared and narrower on the flanks, and also closer spaced. The first three to four major ribs on the body chamber are restricted to the flanks, but towards the aperture, as they become increasingly flared, they bifurcate at the ventral edge and cross the venter as



Fig. 29. A-B. *Tropaeum subsimbirskense compressum* (Sinzow, 1905): SAS EM110 from Manyola Drift, Zululand, Aptian III.  $\times 0,34$ .

very low, broad looped folds. The last three or four ribs before the aperture are the most prominent, being thin and flared on the flanks and broad and high over the venter.

Part of the aperture is preserved. It appears to have been simple, and somewhat constricted.

The suture is very incised and dentritic, consisting of a trifid L, U and I. The lateral lobe is largest and occupies virtually the whole of the flank (see Fig. 87).

#### Dimensions

Specimen	D	Wb	Wh	Wb/Wh	U
SAS EM110	510	140(27)	151(29)	0,93	222(43)
	390	109(27)	139(35)	0,80	163(44)

#### Discussion

The main characteristic features of the phragmocone of this species are the whorl section, with little-inflated flanks, converging to a narrow dorsum (see Förster 1975a, text-fig. 29), and the more or less straight, rursiradiate ribbing. On the body chamber, the low, major costae, separated by wide interspaces and devoid of intercalatories are equally characteristic.

The lectotype (Sinzow 1905, pl. 22 (fig. 1)) specimen does not have quite as prominent major costae as the Zululand or Mozambique material, but it appears that only a part of the body chamber is preserved. The last part of the outer whorl on the lectotype also is slightly detached. Illustrations of *T. bowerbanki* in Casey 1960 (compare pl. 4 (fig. 1) and pl. 5 (fig. 1)), however, show that there is some degree of variation in the tightness of coiling of the outer whorl in *Tropaeum*, and that it can be included in the range of intraspecific variation.

The closest European ally to this species is *Tropaeum bowerbanki* J. de C. Sowerby, from which the present form appears to have been derived. The major differences are that the flanks are more convergent on the phragmocone in *T. subsimbirskense compressum* than in *T. bowerbanki*, whilst the body chamber of *T. bowerbanki* is also more robust; the ribs are flared and high-crested, compared to the low, broad ribs in *T. subsimbirskense compressum*.

As yet no Malagasy equivalent of this species has been described.

Förster (1975a) has shown that specimens occur with a diameter in excess of 900 mm, surpassing all other records of large *Tropaeum*.

#### Occurrence

Upper Aptian of Mangyschlak, southern Russia, Bulgaria?, Mozambique and Zululand.

#### *Tropaeum rossicum* Casey, 1960

Figs 30, 31B

*Ancyloceras gracilis*, Sinzow, 1872: 35, pl. 6 (figs 5-6, 10-11).

*Crioceras gracile* Sinzow, 1905: 306, pl. 17 (figs 1-4), pl. 18 (fig 6), pl. 19 (fig. 1).

*Tropaeum rossicum* Casey, 1960: 43.



*Material*

SAM-PCZ5681 from an unknown locality in Zululand.

*Holotype*

Sinzow's (1905, pl. 18 (fig. 1)) specimen from Stepnaja, Simbirsk.

*Description*

The available specimen consists of just over one whorl. Coiling is loose, with the whorls just touching but not impressed. The whorl section is ovoid,



Fig. 30. *Tropaeum rossicum* Casey, 1960. SAM-PCZ5681 from an unknown locality in Zululand.  $\times 0,57$ .



Fig. 31. A. *Australiceras wandalina* (Boshoff MS) sp. nov. SAS EM106 from Manyola Drift, Zululand, Aptian III.  $\times 0,69$ . B. *Tropaeum rossicum* Casey, 1960. SAM-PCZ5681 from an unknown locality in Zululand.  $\times 0,6$ .

higher than wide on the early part of the whorl, but becomes more rounded on the outer part. Ornament consists of approximately 100 strong, rursiradiate, rounded ribs, separated by interspaces of equal width. Initially, ribbing is quite prominent on the umbilical wall, but eventually becomes quite faint at the largest diameter preserved. The ribs cross the flanks and venter without interruption.

### Discussion

Casey (1960: 43) drew attention to the fact that *Ancyloceras gracile* Sinzow, 1872 was a homonym of *Ancyloceras gracile* Oppel in Zittel 1868 and that a new name was required. Being uncertain as to whether Sinzow's 1872 (pl. 6 (figs 5-6, 10-11)) immature specimens of *Ancyloceras gracile* were conspecific with his (Sinzow's) 1905 specimens of *Crioceras gracile*, Casey designated Sinzow's (1905 pl. 18 (fig. 1)) specimen as holotype of *Tropaeum rossicum*.

With only one specimen available, it is impossible to comment on the relationship of Sinzow's 1872 and 1905 specimens, and the species is here interpreted on the basis of the 1905 specimens. Sinzow (1905, pl. 19 (fig. 1)) illustrated a specimen with finer ribbing with which the Zululand specimen compares well. The whorl section provided by Sinzow (1905: 308) also corresponds to that of the present specimen. No sign of ventral tuberculation is present, but according to Sinzow this only is present in the early and late stages.

*T. rossicum* is easily distinguished by the ovoid whorl section on the phragmocone, the strong, rounded and relatively straight, rursiradiate ribbing. *T. sp. aff. undatum* Whitehouse, to be described below, has similar ornament on the inner whorls, but shows a rapid increase of whorls and a square whorl section. *T. drewi* Casey (1960: 35, pl. 8 (figs 1-2), pl. 9 (fig. 1), text-figs 10, 11f) has a similar rib density (c. 90 at 150 mm diameter), but ribbing is more or less radial and the whorl section compressed.

*Tropaeum caseyi* Collignon (1962: 18, pl. 222 (fig. 965)) has a similar, but much coarser style of ribbing.

By the possession of tuberculation in the early and late stages, *T. rossicum* occupies an intermediate position between *Tropaeum* and *Australiceras*. Casey (1960: 25) refers to *T. rossicum* as being intermediate between *T. hillsi* and *A. gigas*, both forms with a body chamber terminating in a straight shaft and hook. It is not quite clear if this is meant to imply a hook-shaped body chamber in *T. rossicum*. Sinzow's figures and his comparisons with *T. bowerbanki* indicate, rather, that the coiling was aspinoceratid or crioceratitid.

### Occurrence

*T. rossicum* is only known from the Aptian of Simbirsk and Zululand. Casey recorded *Tropaeum cf. rossicum* from the Upper Aptian *martini* Zone of Maidstone, Kent.



*Tropaeum dayi* sp. nov.

Figs 32–34

*Tropaeum* cf. *australe*: Day, 1974: 5, pl. 1 (fig. 1a–b), pl. 2 (fig. 2a–b).*Holotype*

SAS EM109b from Manyola Drift, northern Zululand, Aptian III. Collected by the late Mr E. Meyer.

*Derivation of name*

Named after Dr R. Day, Geological Survey of Queensland, Brisbane.

*Description*

The innermost whorls are not preserved. Coiling is open, crioceratitid, with the whorls not touching. The body chamber becomes a little detached. The whorl section is compressed with a rounded dorsum lacking a zone of impression, a broadly rounded umbilical edge, weakly inflated flanks and a broadly rounded venter. Ornament on the early whorls consists of delicate, thin ribs, separated by wider interspaces. The ribs are straight to sinuous on the flanks and cross the dorsum and venter with a forward curvature. Rib density is *c.* 100 at a diameter of 150 mm. With increasing diameter ribbing becomes coarser, but there is no abrupt change in ornament on the body chamber. On the body chamber of the holotype, of which half a whorl is preserved, twenty-six ribs occur per half whorl. Ribbing on the body chamber is broad and low, with very faint traces of tuberculation on the last few ribs. The aperture is unknown.

The suture is minutely frilled. The lateral lobe is largest, asymmetrical and occupies virtually the whole of the flanks (see Fig. 34).

*Dimensions*

<i>Specimen</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
SAS EM 109b	285	110(28,5)	140(36,3)	0,78	157(40,7)

*Discussion*

Apart from slight differences in relative proportions, the Zululand specimen and the Australian specimen figured by Day (1974: 5, pl. 1 (fig. 1a–b), pl. 2 (fig. 2a–b)) as *Tropaeum* cf. *australe* are virtually identical. Ornament on the inner and outer whorls is the same and both lack a sudden change in ornament at the beginning of the body chamber. The loose coiling is conspicuous in both forms and serves to distinguish it from *T. australe* (Moore). *T. australe* (Moore) is a poorly-known species, but from the available illustrations (Moore 1870, pl. 15 (fig. 3); Etheridge Jun. 1892, pl. 31 (fig. 1), pl. 32 (figs 3–4)) it can be seen that ornamentation and whorl section are similar to those of the present species, but that the coiling is closer with the whorls touching.

*Australiceras rabenjanaharyi* Collignon (1962: 26, pl. 226 (fig. 969)) from Madagascar, has similar ornament after the initial trituberculate stage, but is also tightly coiled with the whorls touching.

*Tropaeum rossicum* Casey, 1960 has a similar whorl shape but ribbing is much coarser and ornament on the body chamber differs from that of *T. dayi* sp. nov.

The presence of faint tubercles on the inner whorl of this species (Day, 1974: 5) indicates that it is somewhat intermediate between *Tropaeum* and *Australiceras*, as is the case in *T. rossicum*.

#### Occurrence

The Australian specimens are from the Aptian of the Eromanga and Surat basins. The Zululand specimen is from the authors' Aptian III.



Fig. 32. *Tropaeum dayi* sp. nov. SAS EM109b, holotype from Manyola Drift, Zululand. Aptian III.  $\times 0,32$ .



Fig. 33. A-B. *Tropaeum dayi* sp. nov. SAS EM109b, holotype from Manyola Drift, Zululand, Aptian III.  $\times 0,42$ .





Fig. 34. *Tropaeum dayi* sp. nov. SAS EM109b. Suture line of holotype.  $\times 1$ .

*Tropaeum obesum* sp. nov.

Figs 35–37, 38D, 39–42, 65E

*Holotype*

SAM-PCZ5681 from locality 34, Zululand. Aptian IV. Housed in the South African Museum. Collector unknown.

*Material*

The holotype and SAS A4000 from locality 34, Aptian IV, and numerous fragments from locality 168, Aptian IV, including BMNH C7885. BMNH C78886–C8887 are from the same horizon at locality 171.

*Description*

Very large, coiling is crioceratitid with the whorls touching and with a dorsal zone of impression. The body chamber remains in contact with the phragmocone. The whorl section is initially subtrigonal, slightly higher than wide with rounded umbilical edges, moderately inflated flanks and a narrow rounded venter. With increasing diameter the whorl section becomes more

inflated and rounded. On the body chamber, which consists of about half a whorl in the holotype, the section becomes depressed.

Ornament is variable, but consists mostly of slightly sinusoidal ribs on the phragmocone. They are generally inclined backward, but may on occasion be radial. Over the dorsum the ribs are reduced to striae with a strong forward curvature. With increasing diameter ribbing becomes coarser, and the body



Fig. 35. *Tropaeum obesum* sp. nov. SAM-PCZ5681, holotype from locality 34, Zululand, Aptian IV. Area between X-X restored.  $\times 0,22$ .



Fig. 36. *Tropaeum obesum* sp. nov. SAM-PCZ5681 holotype from locality 34, Zululand, Aptian IV. Restored part removed.  $\times 0,26$ .





Fig. 37. *Tropaeum obesum* sp. nov. SAS A4000 from locality 34, Zululand, Aptian IV. Inner whorls up to X sculpted in matrix.  $\times c. 0,5$ .

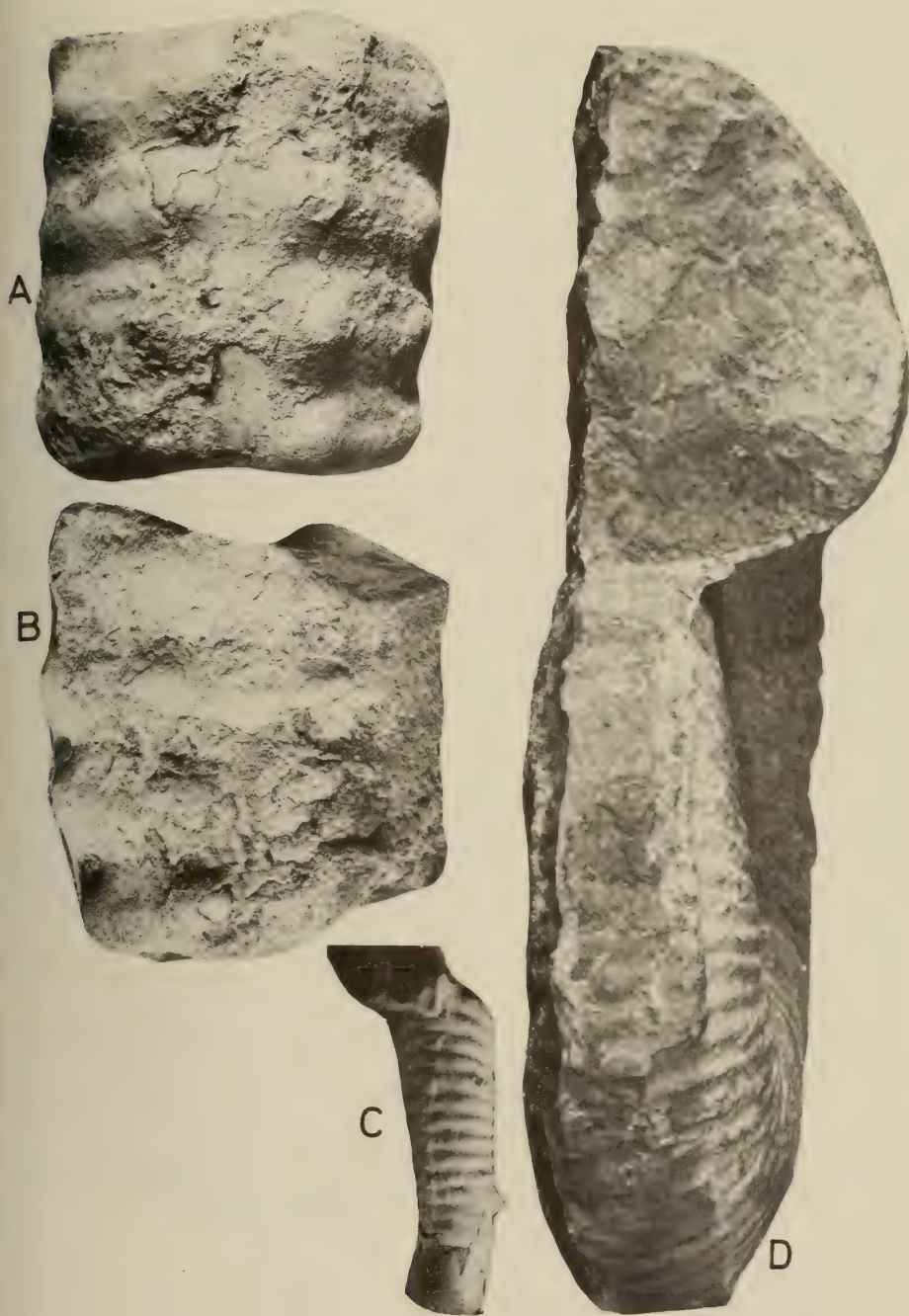


Fig. 38. A-B. *Australiceras* sp. indet. A. SAS L3 from locality 170, Zululand, Aptian I-II.  $\times 1$ . C. *Tonohamites aequicingulatus* (von Koenen, 1902). SAS Z8/Ta1 from locality 168, Aptian III-IV.  $\times 1,5$ . D. *Tropaeum obesum* sp. nov. SAS A4000 from locality 34, Zululand, Aptian IV.  $\times c. 0,5$ .



Fig. 39. A-B. *Tropaeum obesum* sp. nov. BMNH C78886, fragment from locality 171, Zululand, Aptian IV.  $\times 1$ .



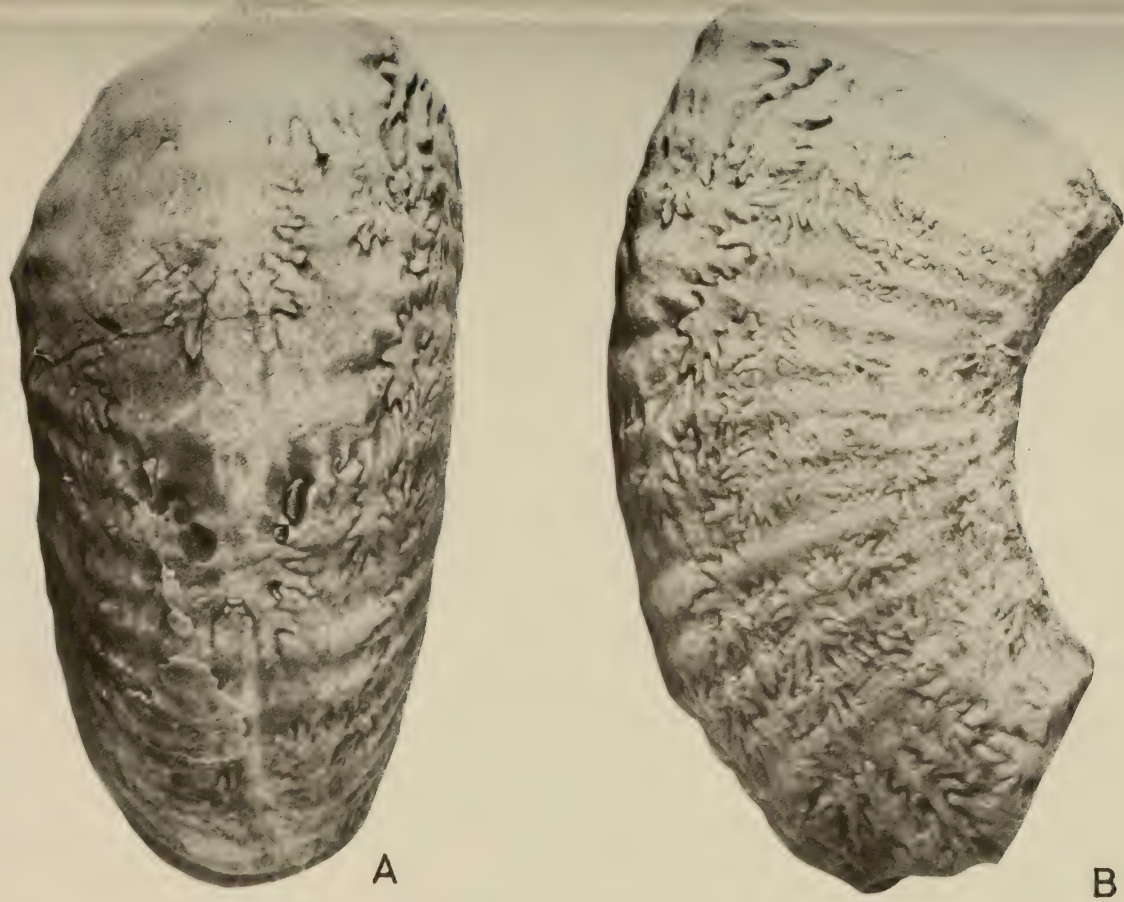


Fig. 40. A-B. *Tropaeum obesum* sp. nov. BMNH C78887, fragment from locality 171, Zululand, Aptian IV.  $\times 0,7$ .



Fig. 41. *Tropaeum obesum* sp. nov. BMNH C78885 from locality 168, Zululand, Aptian IV.  
× 0,9.

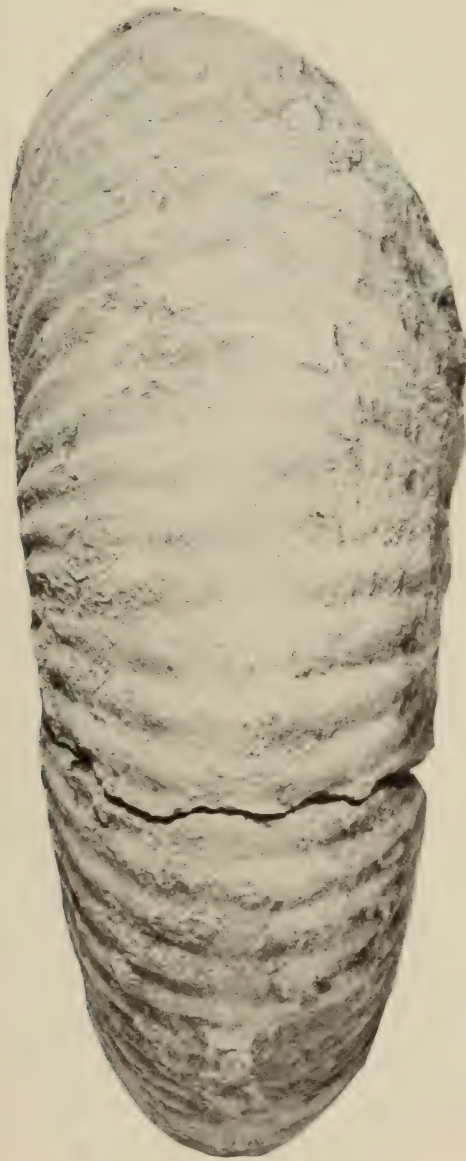


Fig. 42. *Tropaemum obesum* sp. nov. BMNH C78885 from locality 168, Zululand, Aptian IV.  
× 0,9.



chamber bears about twelve heavy, laterally flared, sharp-crested ribs. Over the venter, these ribs are broad and low. Major ribs are also absent on the dorsum and only striae occur.

The suture line is characterized by thin-stemmed saddles and a large asymmetrically trifid lateral lobe.

#### *Dimensions*

<i>Specimen</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
SAM-PCZ5681	630	250(39,9)	210(33,4)	1,18	260(41)

#### *Discussion*

Numerous fragments of *Tropaeum* are tentatively referred to this species which is characterized by its rounded adult whorl section and generally rursi-radiate sinusoidal ribs.

*Tropaeum imperator* Howchin & Whitehouse (1928: 487, figs 144–145) is a similar large species with comparable ornament on the phragmocone. The whorl section on the final whorl, however, is subquadrate, compared to rounded depressed in the present species. Apparently, coiling in *T. imperator* is loosely crioceratitid, whereas that of *T. obesum* sp. nov. is tight, with the inner whorls touching.

*Tropaeum percostatum* (Gabb) (1864: 77, pl. 16 (fig. 26), pl. 17 (fig. 26a)); (see also Anderson, 1938: 212, pl. 71 (fig. 1), pl. 72 (fig. 1) is a related species with denser, lower ribbing on the body chamber. The whorl section of the latter species is subquadrate, compared to rounded-depressed in *T. obesum*. The body chamber of *T. percostatum* is said to become slightly detached.

*Crioceras aegoceras* von Koenen (1902: 328, pl. 36 (figs 1a–c, 2–3)) has similar ornament on the outer whorl, but coarser costation on the inner whorls than *T. obesum* sp. nov., and is only doubtfully referred to *Tropaeum*.

#### *Occurrence*

Upper Aptian of Zululand.

*Tropaeum* sp. aff. *undatum* Whitehouse, 1926

Figs 43–44

#### *Compare:*

*Tropaeum undatum*: Jeletzky, 1964: 68, pl. 20 (fig. 2). Hill, Playford & Woods, 1968: K16, pl. K7 (fig. 3). Day 1974: 6, pl. 3 (figs 2a–b).

*Tropaeum rarum* Whitehouse, 1926: 216, pl. 36 (fig. 1a–b).

#### *Material*

SAS UMS1 from locality 34, Mzinene River. Aptian IV.

#### *Description*

In the Zululand specimen parts of three whorls are still in contact. Coiling is crioceratitid with the whorls just touching. On the innermost whorl the section

is square, but with increasing diameter soon becomes subtrigonal and higher than wide. The dorsum is flat, with a slight dorsal zone of impression on the last whorl, rather sharp umbilical edges and little inflated flanks converging to a broadly rounded venter.

On the innermost whorl still preserved, ornament consists of very strong, broad, slightly rursiradiate single ribs; approximately five in a distance equal to the whorl height. On the succeeding whorl ornament becomes finer, the ribs are weak over the dorsum, crossing it with a slight forward flexure, then passing backwards over the umbilical wall and flexing backwards over the flanks. A few bifurcations occur on the dorsal third of the flanks. Eight ribs occur in a distance equal to the whorl height on the second preserved whorl, and on the last whorl ribbing is very coarse and widely spaced, with five to six ribs per whorl height.



Fig. 43. *Tropaeum* sp. aff. *undatum* Whitehouse, 1926. SAS UMS1 from locality 34, Mzinene River, Zululand, Aptian IV.  $\times 0,52$ .

*Discussion*

*Tropaeum rarum* Whitehouse, 1926 was included in the synonymy of *T. undatum* by Day (1974: 6, 7). The Zululand specimen is tentatively referred to the Australian species because of the similar coarse ribbing on the innermost whorls, followed by slightly sinuous ribbing, together with a rapid increase in whorl diameter. The only obvious difference is that the whorl section of the Australian material is square to depressed, compared to the compressed, higher than wide outer whorl of the Zululand specimen.

*Crioceras australe* Waagen, 1875 *non* Moore, is superficially similar as



Fig. 44. *Tropaeum* sp. aff. *undatum* Whitehouse, 1926. SAS UMS1 from locality 34, Mzinene River, Zululand, Aptian IV.  $\times 0,58$ .



regards the rapid increase in whorl diameter, but is, of course, generically distinct, belonging to *Australiceras*.

The rapid increase in whorl diameter and the coarse ribbing of inner and outer whorls, together with finer ribbing during middle growth stages, clearly distinguish this species from the other Zululand *Tropaeum*.

#### Occurrence

Upper Aptian, Aptian IV of Zululand.

*Tropaeum* sp. gr. ex *bowerbanki* (J. de C. Sowerby) var.

*densistriatum* Casey—*T. hillsi* (J. de C. Sowerby)

Fig. 45

#### Compare:

*Tropaeum bowerbanki* (J. de C. Sowerby) var. *densistriatum* Casey, 1960: 30, pl. 6 (fig. 1).

*Tropaeum hillsi*: Casey, 1960: 30, pl. 7, text-figs 8–9, 11c.

#### Material

SAS L3 from locality 170 Mlambongwenya Creek, Zululand. Lower Aptian, Aptian I or II.

#### Description

One specimen consisting of parts of two embracing whorls is available. Coiling is open, crioceratitid, and the whorls are not in contact. The specimen is slightly crushed, but the whorl section appears to have been rounded-subrectangular, with a rounded venter narrower than the dorsum. The flanks and venter are ornamented by approximately fifty radial ribs per half whorl. The dorsum is smooth and devoid of ribbing.

#### Discussion

The specimen is from the horizon of abundant *Ancyloceras* (*Adouliceras*) spp. The absence of tuberculation on the inner whorl, however, clearly shows that it is a *Tropaeum*.

The whorl section and density of ribbing are the same as those of *Tropaeum bowerbanki* var. *densistriatum* (Casey 1960: 31, pl. 6 (fig. 1)) and *Tropaeum hillsi* (J. de C. Sowerby) (see Casey 1960: 31, pl. 7, text-figs 8–9, 11c). The inner whorls of these two species are indistinguishable (Casey 1960: 33). For the present it is therefore only possible to refer to this specimen as *Tropaeum* sp. gr. ex. *T. bowerbanki* var. *densistriatum*—*T. hillsi*. As Casey has shown (1960: 33) the two species are very close and connected by transitional forms. Because of differences in age, however, he maintained the two species apart.

*Tropaeum subsimbirskense* (Sinzow) (1905: 320, pl. 22 (figs 1–5)) has similar inner whorls, but the flanks are strongly convergent to the venter.

*Occurrence*

*T. hillsi* occurs in the Lower Aptian, top of the *deshayesi* Zone in England. *T. bowerbanki* var. *densistriatum* is ubiquitous in the *bowerbanki* Zone of Kent, England.



Fig. 45. *Tropaeum* sp. gr. ex *bowerbanki* var. *densistriatum-hillsi*. SAS L3 from locality 170, Zululand, Aptian I or II.  $\times 1,1$ .

*Tropaeum* sp. indet.

Fig. 46

*Material*

SAS Z804 from locality 151, Mkuze Game Reserve, Aptian IV.

*Description and discussion*

A massive body chamber fragment, approximately 730 mm long, is of interest in that it is filled with abundant small tonohamitids (to be described below).

The whorl section is wider than high with a slight dorsal zone of impression. Ornament consists of about fifteen heavy, sharp ribs. Ribbing is restricted to the flanks and venter. The dorsum is ornamented by forwardly directed striae, not corresponding in number to the lateral ribs.

Although the inner whorls are not preserved the stratigraphic horizon is one that is characterized by *Tropaeum* with crioceratitid coiling, and the body chamber more or less in contact with the rest of the phragmocone.

The present specimen may be compared with *Tropaeum subarcticum* Casey (1960: 40, pl. 8 (fig. 3a-c), pl. 10 (fig. 1), text-figs 11d, 12) which also grows to great size. Ribbing on *T. subarcticum* is denser, however, and some of the ribs on the body chamber illustrated by Casey (1960: 40, text-fig. 12) are looped, bifurcating near the venter.

*Tropaeum imperator* Howchin & Whitehouse (1928: 487, figs 144-145), another gigantic species from the Aptian of Australia, has much sharper, and more distantly spaced ribbing on the body chamber. *Tropaeum obesum* sp. nov. has a more inflated whorl section and more distantly spaced ribs on the body chamber.

Genus *Australiceras* Whitehouse, 1926

(= *Colombiaticeras* Royo y Gomez, 1945)

*Type species*

*Crioceras jacki* Ethridge Jun., 1880 from the Aptian of eastern Australia by original designation Whitehouse (1926: 208).

*Diagnosis*

Coiling ancyloceratid or aspinoceratid in early Aptian species, but crioceratitid in later ones. Early whorls not always in one plane; ornamented by trituberculate ribs separated by a variable number of intermediaries. Tuberculation ceases at variable diameters in middle stages of growth and may or may not reappear on the body chamber.

*Discussion*

Whitehouse originally introduced *Australiceras* for crioceratitid forms only, a view followed by Wright (1957: L211). Latterly, the genus has been taken to





Fig. 46. *Tropaeum* sp. indet. SAS Z804 from locality 151, Zululand, Aptian IV. Large body chamber fragment with last septum preserved and filled with numerous specimens of *Tono- hamites? caseyi* sp. nov. Photograph by courtesy of Tony Harris (Salisbury).  $\times c. 0,24$ .

include the early Aptian representatives of the lineage with ancyloceratid coiling. The extent and variability of the early Aptian representatives of the genus in the English Lower Greensand was exhaustively reviewed by Casey (1960, 1961), as was the scope of the Australian late Aptian representatives by Day (1974). Unfortunately, however, little or no work has been done on the Central European or Soviet material since the beginning of the century.

Spath (1931: 656) advocated that the name *Australiceras* be abandoned in favour of *Tropaeum*, due to the difficulty encountered in deciding whether or not tuberculation was present, especially in fragmentary material. Transitional forms do occur, for example *Australiceras pingue* Casey, *T. rossicum* Casey, and *T. imperator* Howchin & Whitehouse, but both genera are accepted as valid taxa. For a further discussion on the differences between *Tropaeum* and *Australiceras*, see Casey (1960: 40, 1961: 45). Day's (1974: 8) assertion that the saddles of the suture lines of the Australian representatives of *Australiceras* tend to be broader than those in *Tropaeum* is also true to a certain extent in the Zululand material, and it appears that in some late Aptian species the saddles tend to become broader, accompanied by a general simplification of the suture line.

Differences between the homoeomorphic *Ancyloceras* (*Adouliceras*) and the early uncoiled forms of *Australiceras* are discussed elsewhere (p. 226).

As in *Tropaeum*, three species groups are recognized, based on the coiling.

- (i) *Australiceras* gr. ex. *gigas* (J. de C. Sowerby)
- (ii) *Australiceras* gr. ex. *tuberculatum* (Sinzow)
- (iii) *Australiceras* gr. ex. *jacki* (Etheridge)

Specific differentiation is a moot point, as it is in *Tropaeum*. Virtually all the species described from the Eurasian, Australian, North American, South American and Madagascan regions appear to be endemic to these regions, and either based on unique type specimens, or, if based on large collections, are interpreted so widely that differences between the various species are difficult to formulate, all of which suggests a superfluity of specific names, and high intraspecific variability.

The diameter at which tuberculation ceases is variable, as has been illustrated in *A. gigas* (see Casey 1961: 47) and *A. jacki* (see Day 1974: 9). Rib density and whorl section in the early stages seem to be equally unreliable specific characters in *A. jacki* as shown by Day (1974: 9) and also here in Figures 47–49, based on Australian material housed in the British Museum (Natural History).

The only apparent differences of use in specific separation are the coiling of the body chamber, whorl section, and rib density in the adult stage together with, to a lesser degree, strength of tuberculation and the number of intermediaries in the early stages.

Species to be referred to *Australiceras* are as follows:

1. *Australiceras argus* Anderson (1938: 211, pl. 70 (figs 1–2)).
2. *Australiceras australe* (Waagen *non* Moore) (1875: 246, pl. 60 (fig. 1)).



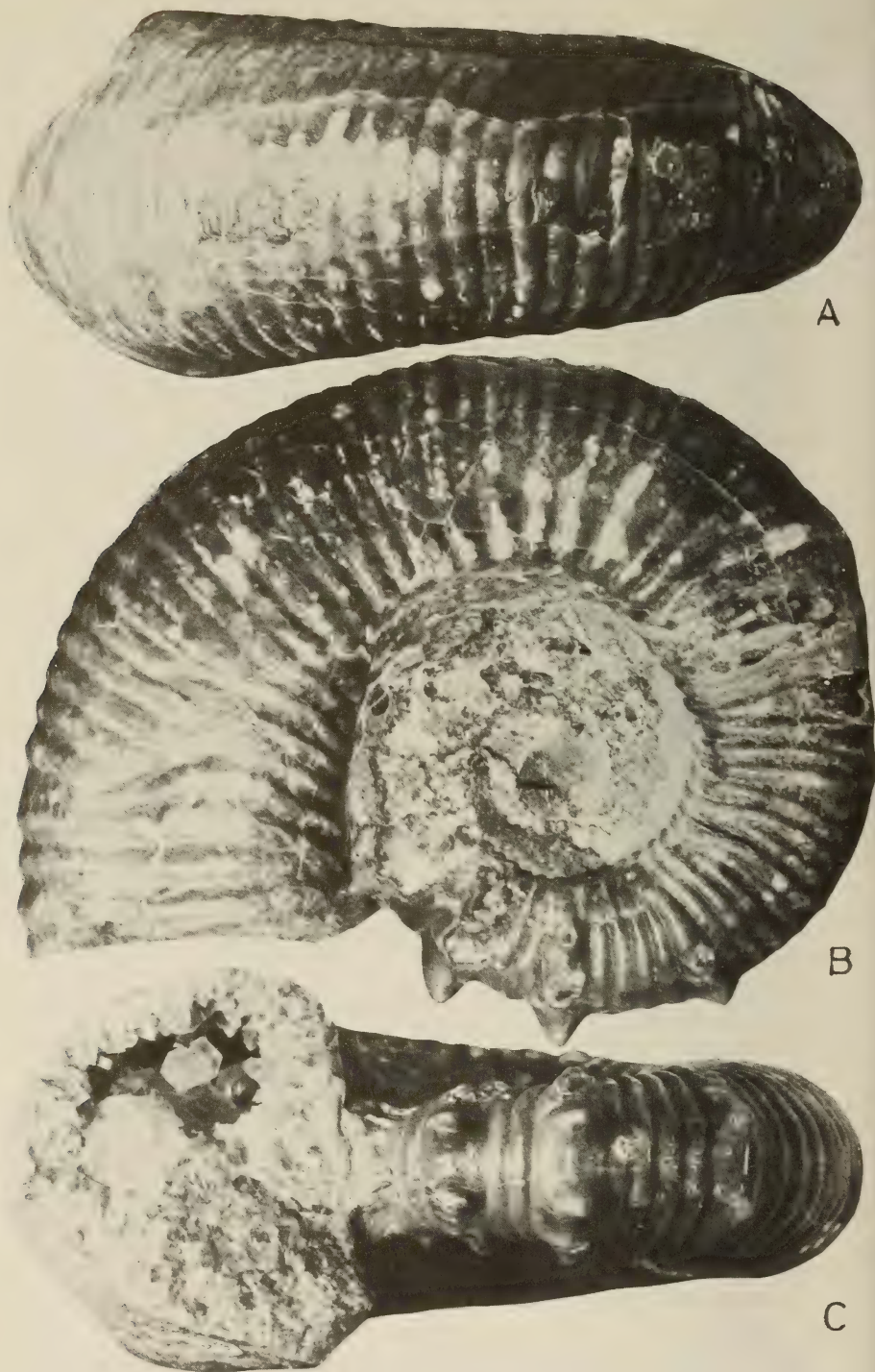


Fig. 47. *Australiceras jacki* (Etheridge Jun., 1880). BMNH C40769 from the Aptian of Rolling Downs, Queensland, Australia.  $\times 1$ .





Fig. 48. *Australiceras jacki* (Etheridge Jun., 1880). BMNH C40760 from the Aptian of Rolling Downs, Queensland, Australia. Note the pathological body chamber.  $\times 1$ .

3. *Australiceras bolivari* (Royo y Gomez) (1945: 470, pl. 75 (fig. 2)).
4. *Australiceras? bulgaricum* Dimitrova (1967: 62, pl. 30 (fig. 1)).
5. ? *Crioceras deecke* Favre (1908: 636, pl. 36 (fig. 4), pl. 37 (fig. 1), text-fig. 7).
6. ? *Crioceras carinato-verrucosum* Sinzow (1905: 316, pl. 21 (figs 1–2)).
7. *Australiceras gigas* (J. de C. Sowerby) (1828: 188, pl. 593 (fig. 2)).
8. *Australiceras gigas* (Sow.) var. *anguimanum* Casey (1961: 52, pl. 13).
9. *Australiceras gigas* (Sow.) var. *arcuatum* Casey (1961: 52, pl. 12 (fig. 1a–c)).
10. *Australiceras gigas* (Sow.) var. *inscriptum* Casey (1961: 52, text-fig. 17).
11. *Australiceras? hirtzi* Collignon (1962: 19, pl. 223 (fig. 966), pl. 244 (fig. 967), pl. 225 (fig. 968)). (According to Förster 1975a: 57 these are actually specimens of *Ammonitoceras pavlowi* Wassiliewski, 1908.)
12. *Australiceras irregulare* (Tenison Woods) (1883: 151, pl. 8 (fig. 2)).



Fig. 49. *Australiceras robustum* Whitehouse, 1926. BMNH C25357, paratype from the Upper Aptian of Flinders River, North Queensland, Australia.  $\times 1$ . (See Whitehouse 1926: 211.) According to Day (1974: 9–10) *A. robustum* may be included in the synonymy of *A. jacki*.

13. *Australiceras jacki* (Etheridge Jun.) (1880: 305, pl. 17 (figs 55–58)).
14. *Australiceras lamprum* (Etheridge Jun.) (1909: 157, pl. 48 (figs 1–2)).
15. *Australiceras laticeps* (Sinzow) (1905: 314, pl. 19 (figs 2–4)).
16. *Australiceras pingue* Casey (1961: 55, pl. 14 (fig. 1), pl. 15 (fig. 1), text-fig. 18b).
17. *Australiceras rabenjanaharyi* Collignon (1962: 26, pl. 226 (fig. 969)).
18. *Australiceras?* *ramboulai* Collignon (1962: 30, pl. 228 (fig. 970)).  
(According to Förster 1975a: 158–9 this is an *Ammonitoceras*.)



19. *Australiceras ramososeptatum* (Anthula) (1899: 127, pl. 14 (fig. 4)).
20. ? *Crioceras sarasini* Favre (1908: 638, pl. 36 (figs 1-3), pl. 37 (fig. 2)).
21. *Australiceras tuberculatum* (Sinzow) (1905: 309, pl. 19 (figs 5-6), pl. 20 (figs 4-5)).
22. *Australiceras tuberculatum* var. *graciloides* (Sinzow) (1905: 312, pl. 20 (figs 1-3)).
23. ? *Ancyloceras urbani* Neumayr & Uhlig (1881: 190, pl. 49 (fig. 3), pl. 50 (fig. 1)).

### Occurrence

*Australiceras* occurs in the Aptian of England, France, northern Germany, Bulgaria?, the caucasian and transcaspian regions of the U.S.S.R., India, Columbia, California, Patagonia?, Australia, Madagascar, Mozambique and Zululand. Neocomian reports from Japan (Matsumoto 1947) have been disproved by Day (1969: 158). However, since then Obata *et al.* (1975) recorded *Australiceras* aff. *gigas* from the Chosi Group of Japan. Dimitrova's (1967: 62, pl. 30 (fig. 1)) *Australiceras bulgaricum* cannot be referred to the genus with certainty.

### *Australiceras ramososeptatum* (Anthula, 1899)

#### Figs 50-52

*Crioceras ramososeptatum* Anthula, 1899: 127, pl. 14 (fig. 4). *Non* Sinzow 1905: 249, pl. 1 (figs 1-3).

*Ancyloceras* sp. Krenkel, 1910: 154.

*Crioceras* aff. *ramososeptatum*: Kasansky, 1914: 40, pl. 1 (fig. 10).

*Ancyloceras ramososeptatum*: Rouchadze, 1933: 220, pl. 9 (fig. 1).

? *Ammonitoceras ramososeptatum*: Drushchitz & Kudryavtsev, 1960: 249, pl. 39 (fig. 1).

*Toxoceratoides royerianus*: Wachendorf, 1967: 290, pl. 35 (figs 1, 4, *non* fig. 5).

*Australiceras ramososeptatum*: Förster, 1975a: 153, pl. 3 (figs 1-2), text-fig. 30.

### Holotype

The specimen figured by Anthula (1899, pl. 14 (fig. 4a)), here refigured as Figure 51. Original at Palaeontological Institute Uppsala University (Sjörögen Collection).

### Material

SAS L7 (3) from the upper part of the section at locality 170, Mlambongwenya Creek, Zululand. Aptian I.

### Description

The available specimen consists of one and a third whorls, but is sufficiently well preserved to illustrate the australiceratid characteristics. Coiling is crioceratid with the whorls touching, but not impressed. The whorl section is subquadrate to rounded in the early stages of growth, but soon becomes triangular with a flattened dorsum, a steep umbilical wall and gently inflated flanks, converging to a rounded venter.





Fig. 50. *Australiceras ramososeptatum* (Anthula, 1899). SAS L7(3) from the upper part of the section at locality 170, Zululand, Aptian I.  $\times 1,1$ .



Fig. 51. *Australiceras ramososeptatum* (Anthula, 1899). The original of Anthula's (1899, pl. 14 (fig. 4a)) *Crioceras ramososeptatum*. Housed in the Palaeontological Institute, Uppsala University (Sjörger Coll.). Photograph supplied by Dr P. Bengtson (Uppsala). Slightly reduced.

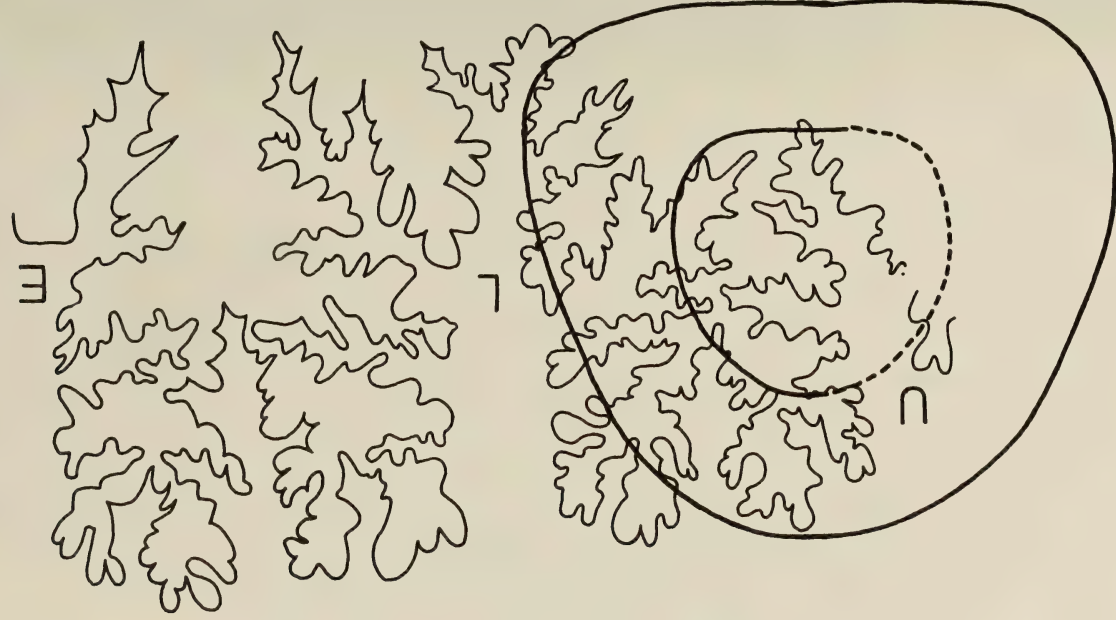


Fig. 52. *Australiceras ramososseptatum* (Anthula, 1899). SAS L3(7). Whorl section  $\times 1$  and suture line  $\times 3$ .



At a whorl height of approximately 20 mm, ornament consists of alternate trituberculate ribs and non-tuberculate intermediaries. The tuberculate ribs are much stronger than the intermediaries, being about twice as wide. The ventral tubercles are largest, and situated a little distance from the siphonal line. The lateral tubercles are on the ventral third of the flanks. The umbilical tubercles are smallest and either pointed or elongated in the direction of ribbing.

After about a third of a whorl tuberculation disappears rather suddenly, and ornament consists of slightly rursiradiate ribs only, separated by interspaces of similar width. Occasional bifurcations occur at midflank.

The outer whorl is abraded and encrusted by epizoans, but appears to have borne similar ribs. The suture line is very incised, with a large asymmetrical trifold lateral lobe which covers virtually the whole of the flanks. The saddles are very narrow-stemmed.

#### Dimensions

Specimen	D	Wb	Wh	Wb/Wh	U
SAS L7 (3)	87,5	36(41,1)	36(41,1)	1	39(44,5)
	155	73(47,1)	66(42,5)	1,1	c. 65(41,9)

#### Discussion

The strong tuberculation on the inner whorl, combined with the steep umbilical wall on the outer whorl are characteristic of the species. Anthula (1899: 127) mentioned the presence of intermediary, non-tuberculate ribs which may appear regularly or sometimes be absent. This, however, does not feature prominently in Anthula's illustration or in the holotype here refigured as Figure 51.

Some subsequent references of material to Anthula's species appear to be incorrect. Sinzow's (1915, pl. 11 (figs 1-3a)) *Crioceras ramososeptatum* (especially fig. 1) has distinctly looped and ventrally bifurcating ribs, and should probably be referred to *Ammonitoceras*. The specimen figured by Drushchitz & Kudryavtsev (1960: 294, pl. 39 (fig. 1)) as *Ammonitoceras ramososeptatum* has finer ribbing than Anthula's species, and indeed appears to be *Ammonitoceras*.

*Crioceras jackii* Etheridge Jun. (see Figs 47-49), especially Etheridge's specimen (1909, pl. 35 (fig. 1)), is close to the present species, but differs mainly in having finer ribbing, more intermediaries during the tuberculate stage, and more bifurcating ribs in the non-tuberculate stage.

*Crioceras australe* Waagen *non* Moore (1875: 246, pl. 60 (fig. 1a-c)) is slightly similar, but has a rounded whorl section and a dorsal zone of impression.

*Australiceras argus* Anderson (1938: 211, pl. 70 (figs 1-2)) is similar in having alternate tuberculate and non-tuberculate ribs on the inner whorls, but has coarser ribbing and an ovoid whorl section on the outer whorl.

*Australiceras lampros* (Etheridge Jun.) has a similar triangular whorl section (see Whitehouse 1926, pl. 35 (fig. 1b)), but is only weakly trituberculate in early stages of growth.

*Occurrence*

Lower Aptian of southern Russia, Mozambique and Zululand.

*Australiceras* sp. aff. *A. irregulare* (Tenison Woods, 1883)

Figs 65C–D, 68F, 80A

*Compare:*

*Crioceras irregulare* Tenison Woods, 1883: 151, pl. 8 (fig. 2). Etheridge Jun. 1892: 501, pl. 33 (fig. 1), pl. 42 (fig. 16).

*Crioceras jackii* Etheridge Jun., 1909: 145 (*pars*), pl. 35 (fig. 1), pl. 36 (fig. 1), pl. 37 (fig. 2).

*Australiceras irregulare*: Whitehouse, 1926: 210, pl. 37 (fig. 1a–b). Day, 1974: 10, pl. 2 (fig. 3), pl. 6 (figs 1–2a–c), text-figs 3A, C. (With complete synonymy.)

*Material*

SAS 63/2, SAS LJE183; SAS Z8/2 from locality 168 and BMNH C79714 from locality 167, Mfongozi Creek, Aptian III–IV.

*Description*

A small *Australiceras*, with slightly elliptical, crioceratitid coiling. The whorls touch, but are not impressed. The whorl section is initially rounded, but progressively becomes higher than wide. The initial whorls, at a whorl height of approximately 5,5 mm, are ornamented by narrow widely spaced prorsiradiate ribs, apparently lacking tubercles. At a whorl height of approximately 7 mm, every second rib is strengthened and tubercles appear, and by a whorl height of 10 mm tuberculation is already quite prominent. The ventral tubercles are largest, and the umbilical ones smallest. The distance between the umbilical and lateral tubercles is greater than that between the latter and the ventral tubercles. The shape of tubercles is variable, the ventral ones are usually round and bullate, whereas the lateral and umbilical ones are elongated in the direction of ribbing in the early stages, but eventually also become slightly rounded. Non-tuberculate intermediaries vary from one in the initial stages to up to three, although there are normally only two in later growth stages. Ribbing is continuous, though weakened over the dorsum.

*Dimensions*

<i>Specimen</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
SAS 63/2	64,6	c. 20(c. 31)	20,5(32)	c. 0,86	32(50)

*Discussion*

The scope of *Australiceras irregulare* (Tenison Woods) has been extended so far by Day (1974: 10) that the Zululand material may be tentatively referred to that species. *A. irregulare* has initial whorls with either weak or no tuberculation, and, as Day (1974, pl. 2 (fig. 3)) has shown, they are not always coiled

in one plane. On the basis of the material available, a definite identification is not possible. The specimens are of some importance though, for they may point to the origin of *Helicancyloceras* gen. nov., to be described below.

*Crioceras* (*Ancyloceras*) *matheroni* in Pavlow (1890: 4, pl. 6 (fig. 2a-b)) bears superficial resemblance to the present species, but is too poorly known for further comment.

#### Occurrence

Upper Aptian of Zululand.

*Australiceras wandalina* (Boshoff MS.) sp. nov.

Figs 6B, 53-57, 61D

#### Holotype

UPG-B8 (Boshoff Collection), Department of Geology, University of Pretoria, from the Upper Aptian of Manyola Drift, northern Zululand, Aptian III. Collected by J. C. Boshoff. (Unpublished thesis 1945.)

#### Material

Paratype SAS EM106 is from Manyola Drift, Aptian III, Paratype BMNH C78888 is from the Upper Aptian of Mlambongwenya Spruit.

#### Description

The specimens are still septate at the largest diameters preserved, but judging by the rather tight coiling, it appears unlikely that the body chamber becomes detached. The initial whorl section is suboctagonal, slightly higher than wide, but eventually becomes subrectangular with a rounded venter and a slight dorsal zone of impression (Fig. 6B).

At the smallest preserved diameter ( $Wh = 25$  mm), ornament consists of straight, radial ribs arising at the umbilical edge, each bearing three rows of pointed tubercles. The umbilical and lateral ones are situated on the dorsal and ventral thirds of the flanks respectively; the ventral ones are a little distance away from the siphonal line. All the tubercles are pointed and elongated in the direction of ribbing to a certain extent. With increasing diameter ribbing becomes blunter and the tubercles more bullate. The umbilical tubercles disappear at a diameter of *c.* 225 mm, whereas in some specimens the lateral ones, which have now migrated closer to the venter, become indistinct at a diameter of 240 mm. The ventral tubercles persist as swellings on the ventral part of the ribs to much greater a diameter.

On the inner whorl, the rib density is forty-nine per whorl and intermediaries seem to be absent. On the outer whorl, rib density is fifty-one per whorl and two intermediaries occur.

The suture line, despite decortication, appears very simple, with large and asymmetrically trifid lobes. The lateral lobe is largest and occupies virtually the whole of the flanks.





Fig. 53. *Australiceras wandalina* (Boshoff MS) sp. nov. UPG B8, holotype from Manyola Drift, Zululand, Aptian III.  $\times 0,44$ .



Fig. 54. *Australiceras wandalina* (Boshoff MS) sp. nov. UPG B8, holotype from Manyola Drift, Zululand, Aptian III,  $\times 0,44$ .





Fig. 55. *Australiceras wandalina* (Boshoff MS) sp. nov. SAS EM106 from Manyola Drift, Zululand, Aptian III.  $\times 0,59$ .



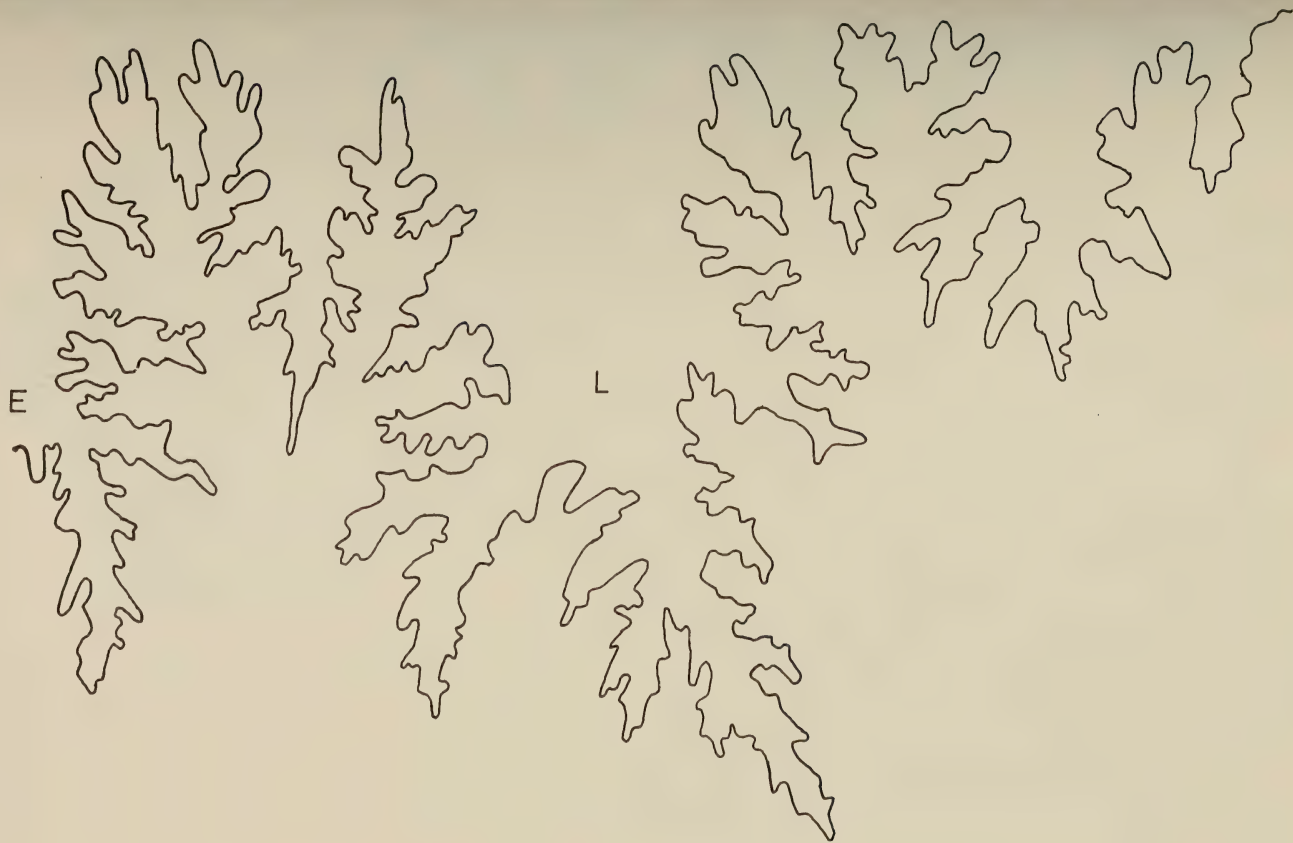


Fig. 56. *Australiceras wandalina* (Boshoff MS) sp. nov. UPG B8. Suture line  $\times 1$ .



Fig. 57. *Australiceras wandalina* (Boshoff MS) sp. nov. BMNH C78888 from locality 171, Zululand. Found loose. Specimen with much finer ribbing on inner whorls, probably representing a new subspecies.  $\times 0,67$ .

*Dimensions*

<i>Specimen</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
UPG-B8	373	134(36)	144(38,6)	0,93	160(43)

*Discussion*

The strong ornamentation on the inner whorls, combined with the persistence of ventral tubercles to such a large diameter, characterize the species.

A single specimen (BMNH C78888 from locality 171 found loose on the surface (Fig. 57)) and consisting of less than half of two successive whorls has fine ribbing on the inner whorls, c. eighty per whorl, but ornament comparable to that of *A. wandalina* on the outer whorl, and may possibly represent a new subspecies.

Amongst Madagascan species, *Australiceras hirtzi* Collignon (1962: 19, pl. 223 (fig. 966), pl. 224 (fig. 967), pl. 225 (fig. 968)), has comparable inner whorls and relative proportions. It differs from *A. wandalina*, however, in losing its ventral tubercles at a relatively early stage, and in having finer ribbing on the outer whorl. (See Collignon 1962, pl. 225 (fig. 968).)

*Australiceras rabenjanaharyi* Collignon (1962: 26, pl. 226 (fig. 969)) has finer ornament both on the inner and outer whorls. *Australiceras? ramboulai* Collignon (1962: 30, pl. 228 (fig. 970)) has whorls increasing very slowly in size, and a curious ornament of ribs bifurcating from the umbilical tubercles in the later stages. As Förster (1975a: 158) has shown, this species is probably synonymous with *Ammonitoceras pavlowi* (Wassiliewski 1908: 46, pl. 3 (fig. 1a-c)).

Retention of tubercles to such a large diameter is reminiscent of '*Crioceras*' *deecke*i Favre (1908: 636, pl. 36 (fig. 4), pl. 37 (fig. 1), text-fig. 1) and '*Crioceras*' *sarasini* Favre (1908: 638, pl. 36 (figs 1-3), pl. 37 (fig. 2)) and the Zululand specimen to be described below as *Australiceras?* sp. cf. '*Crioceras*' *sarasini* Favre. The Patagonian species, whatever their generic identity, however, have much stronger tuberculation than the present species.

*Occurrence*

Upper Aptian of Zululand.

*Australiceras?* sp. cf. '*Crioceras*' *sarasini* Favre, 1908

Fig. 10A

*Compare:*

*Crioceras sarasini* Favre, 1908: 638, pl. 36 (figs 1-3), pl. 37 (fig. 2).

*Material*

SAS H71D/18 from Nhlohlela Pan, Mkuze Game Reserve, locality 150, Aptian III-IV.

*Description*

A small septate fragment, 130 mm long, is comparable with the larger end of the outer whorl of the original of Favre's pl. 36 (figs 1-2). The intercostal



section is rounded subtriangular with a flat dorsum and moderately inflated flanks converging to a narrow venter. Maximum width is at the dorsal third of the flanks. Ornament consists of five strong, rounded, radial ribs, bearing three rows of tubercles on either side. The dorsum is smooth and devoid of ribbing. There is a distinct depression along the venter between the tubercles where ribbing is interrupted.

#### Discussion

As mentioned above, there is striking similarity between the Zululand specimen and the larger end of Favre's '*Crioceras*' *sarasini*. The only apparent difference is that the umbilical tubercles in the Patagonian species are larger, and that the ribs are wider spaced. However, on the basis of the limited material, a definite specific allocation is impossible. Both '*Crioceras*' *sarasini* Favre and '*Crioceras*' *deecke*i Favre are of enigmatic generic affinity. Spath erected the genus *Peltocrioceras* for '*Crioceras*' *deecke*i which 'requires a new generic designation' (Spath 1924: 85). Neither then, nor later, was any generic diagnosis given by Spath, and whether '*Crioceras*' *sarasini* was to be included in *Peltocrioceras* or not was never specified. Riccardi (1971: 277) regards both species as being representatives of *Peltocrioceras*, but as being close to both *Tropaeum* and *Australiceras*. Leanza (1963: 221) and Day (1974: 6) (the latter in comparing '*Crioceras*' *deecke*i with *Tropaeum imperator* Howchin & Whitehouse) both indirectly suggested that *Peltocrioceras* might be a junior synonym of *Tropaeum*. Wiedmann (1962: 112) regarded *Peltocrioceras* as a synonym of *Crioceratites*. '*Crioceras*' *sarasini* differs from '*Crioceras*' *deecke*i mainly in having weaker lateral tuberculation on the inner whorls, and in having interrupted ribbing over the venter, ending in strong nodes. Both species belong to the same genus, which appears to bear superficial similarity to both *Tropaeum* and *Australiceras*.

*Australiceras wandalina* sp. nov. is superficially similar in retaining tuberculation to large diameters, but has denser ribbing and the tubercles are not as strong.

*Australiceras ramboulai* Collignon (1962: 30, pl. 227 (fig. 970)) has a similar whorl section, but lacks the strong ornament.

#### Occurrence

'*Crioceras*' *sarasini* is of Aptian age, and not Barremian as Favre (1908) and Piatnitzky (1938) had incorrectly assumed. The Zululand specimen is of Upper Aptian age, Aptian III-IV.

*Australiceras*? sp. indet. A.

Fig. 38A-B

#### Description and discussion

A septate fragment, SAS L3 from locality 170, and of Lower Aptian age, has an octagonal whorl section and four trituberculate ribs, and is referred to

*Australiceras* with doubt. Ribbing is radial on the flanks, interrupted over the venter and absent on the dorsum. The fragment is possibly allied to *A. wandalina* sp. nov. and *A.* sp. cf. '*Crioceras*' *sarasini* Favre in being strongly tuberculate at large diameters.

*Ammonitoceras pavlowi* (Wassiliewski, 1908), described and figured from Mozambique by Förster (1975a: 156, pl. 3 (figs 5–7)), has a similar whorl section, but differs in having regular ventrally bifurcating or intercalatory ribs.

*Australiceras*? sp. indet. B.

Fig. 58A–B

#### *Description and discussion*

A curved body chamber fragment, SAS 54/45 from the Lower Aptian at locality 170 below the horizon of abundant *Ancyloceras* (*Adouliceras*) with flared, trituberculate ribs, may possibly belong to the uncoiled forms of genus *Australiceras*. The whorl section is ovoid, depressed, with a little-rounded dorsum and strongly rounded flanks and venter. Five flared ribs with distinct ventral but indistinct lateral and umbilical tubercles are present. The dorsum is ornamented by faint striae.

The strongly depressed whorl section recalls Sinzow's *Crioceras laticeps* (1905: 314, text-fig. 3, pl. 19 (figs 2–4)). In Sinzow's species, however, rib density is less than in the present specimen. Specimens of *Australiceras gigas* (J. de C. Sowerby) sometimes also show such flared ribs in the crozier, but again, the rib density is lower.

#### Subfamily Helicancylinae Hyatt, 1894

Hyatt's family Helicancyllidae was revived by Casey (1961: 76, as Helicancylinae) 'as a useful subfamily term for those diminutive ancyloceratids in which the sculpture is simplified on the terminal hook'.

The subfamily, as interpreted by Casey, is here accepted with reservation as a useful grouping of three genera only: *Tonohamites* Spath, 1924, *Toxoceratoides* Spath, 1924, and *Helicancyllus* Gabb, 1869, although *Acrioceras* Hyatt, 1900, *Lytocrioceras* Spath, 1924, and *Leptoceras* Uhlig 1883, have also tentatively been referred to the sub-family.

Apart from the fact that the type genus is difficult to interpret (see Casey 1961: 77), transitional forms occur, linking the genera. Classification is based mainly on the mode of ribbing on the body chamber and, to a lesser extent, the presence or absence of (tri-)tuberculation on the phragmocone.

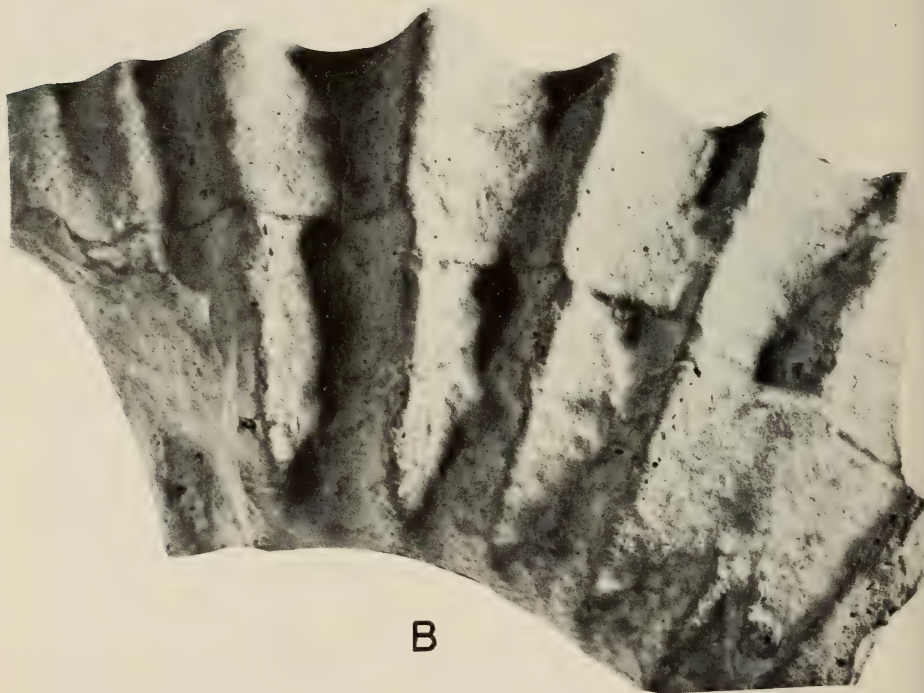
#### Genus *Toxoceratoides* Spath, 1924

##### *Type species*

*Toxoceras royerianum* d'Orbigny, 1842 from the Lower Aptian of France.



A



B

Fig. 58. *Australiceras?* sp. ind. B. SAS 54/45 from locality 170, Zululand, Aptian I.  $\times 1$ .



### Diagnosis

Small forms with ancyloceratid or leptoceratid coiling, probably with an initial helix. Trituberculate ribs occur on the phragmocone but disappear on the recurved hook.

### Discussion

The genus was discussed extensively by Casey (1961: 79) and little can be added. Differences between *Toxoceratoides* and *Tonohamites* are slight, and trituberculate forms such as *Tonohamites decurrens* connect the two genera.

The following species were referred to genus *Toxoceratoides* by Casey (1961):

1. *Toxoceratoides biplex* (von Koenen) (1902: 381, pl. 41 (figs 3, 10a-b, 11a-b)).
2. *Toxoceratoides caucasicus* (Kasansky) (1914, pl. 1 (fig. 8a-c)).
3. *Toxoceratoides fustiformis* (von Koenen) (1902: 384, pl. 41 (figs 4-5, 7a-c, 9a-b), pl. 53 (figs 8a-b, 9a-b)).
4. *Toxoceratoides obliquatus* (Young & Bird) (1828: 278, pl. 18 (fig. 11)).
5. *Toxoceratoides proteus* (Spath) (1930: 461, pl. 16 (fig. 7)).
6. *Toxoceratoides rochi* Casey, 1961 (= *Ancyloceras royerianum* in Roch 1927: 30, pl. 1 (fig. 4)).
7. *Toxoceratoides rotundus* (Phillips) (1875: 264, pl. 1 (fig. 24)).
8. *Toxoceratoides royerianum* (d'Orbigny) (1842: 481, pl. 118 (figs 7-11)).
9. *Toxoceratoides seminodosus* (Roemer) 1841.
10. *Toxoceratoides sheperdi* (Spath) (1942: 173, figs 5-6).

To this list may be added:

11. *Toxoceratoides biplicatum* (von Koenen) (1902: 379, pl. 41 (figs 2a-b, 8a-b)).
12. *Toxoceratoides krenkeli* Förster (1975a: 160, pl. 4 (figs 1-2), text-fig. 33a-b).
13. *Toxoceratoides saulae* Murphy (1975: 31, pl. 4 (figs 4, 6)).
14. *Toxoceratoides starrkingi* (Anderson) (See Murphy 1975: 32, pl. 4 (figs 3, 5)).
15. *Toxoceratoides corae* Murphy (1975: 33, pl. 5 (figs 1, 5)).
16. ? *Toxoceratoides greeni* Murphy (1975: 33, pl. 5 (figs 2-3, 6)).
17. *Toxoceratoides* spp. indet. described by Murphy as *Toxoceratoides* sp. 1 (1975: 35, pl. 6 (figs 1-2, 11)) and ?*Toxoceratoides* sp. (1975: 35, pl. 3 (fig. 6), pl. 6 (figs 5-6)).
18. *Toxoceratoides* sp. nov. Thomson (1974: 16, pl. 3a, d).

### Occurrence

*Toxoceratoides* ranges from the Upper Barremian to Upper Aptian, and is known from Europe, California and south-east Africa. Reports from Australia are not accepted here. '*Ancyloceras*' *taylori* Etheridge, referred to *Toxoceratoides* by Whitehouse (1926: 216) is a doubtful contender, as are the five specimens described by Day (1974: 13) as *Toxoceratoides* ? spp.

*Toxoceratoides royerianus* (d'Orbigny, 1842)

Fig. 59E

*Toxoceras royerianus* d'Orbigny, 1842: 481, pl. 118 (figs 7–11).? *Toxoceras emericianus* d'Orbigny, 1842: 487, pl. 120 (figs 5–9).*Toxoceratoides royerianus*: Casey, 1961: 78, pl. 6 (fig. 2a–b), pl. 17 (fig. 3a–b), text-fig. 30a–h) (cum synon.).*Neotype*

The specimen figured in Casey (1961, text-fig. 30a–c) from the Lower Aptian of Haute Marne, France, and in the collections of the Sorbonne, Paris.

*Material*

SAM-PCM5313 from Lubemba, southern Mozambique.

*Description*

A recurved crozier with part of the phragmocone is referred to the species.

The part of the phragmocone preserved on the recurved crozier is heavily abraded and only umbilical tubercles are preserved. At the apertural end of the crozier the whorl section is ovoid, with a flattened dorsum, sharp umbilical edge and broadly rounded venter. Ornament consists of relatively narrow, high ribs, separated by deep interspaces which are wider than the ribs. The ribs arise in groups of two or three from the umbilical tubercles. They are prorsiradial at the proximal end of the crozier, but become radial on the bend of the crozier and at the distal end. At the apertural end a pair of single ribs arises from the umbilical tubercles.

*Discussion*

The recurved crozier compares well with the illustrations and figures provided by Casey (1961), who also discussed the species extensively.

*Toxoceratoides krenkeli* Förster, 1975a differs from *T. royerianus* mainly in having hardly any intermediary ribs on the shaft, and in having coarser ribbing on the crozier.

*Occurrence*

Lower Aptian of western and central Europe, Mozambique and Zululand.

*Toxoceratoides krenkeli* Förster, 1975

Fig. 59F

*Hamites royerianus*: Kilian, 1902: 465.*Ancyloceras royerianum*: Krenkel, 1910: 151, pl. 17 (figs 12–13).*Tonohamites royerianum*: Haughton & Boshoff, 1956: 13, pl. 2 (fig. 3).*Acrioceras dissimilis*: Wachendorf, 1967: 281, pl. 35 (figs 2–3), text-fig. 5.*Toxoceratoides royerianus*: Wachendorf, 1967: 290, pl. 35 (fig. 5, non figs 1, 4).*Toxoceratoides krenkeli* Förster, 1975a: 160, pl. 4 (figs 1–2) text-fig. 33a–b.*Holotype*

Wachendorf's (1967, pl. 35 (fig. 2)) specimen from Chalala, Mozambique.

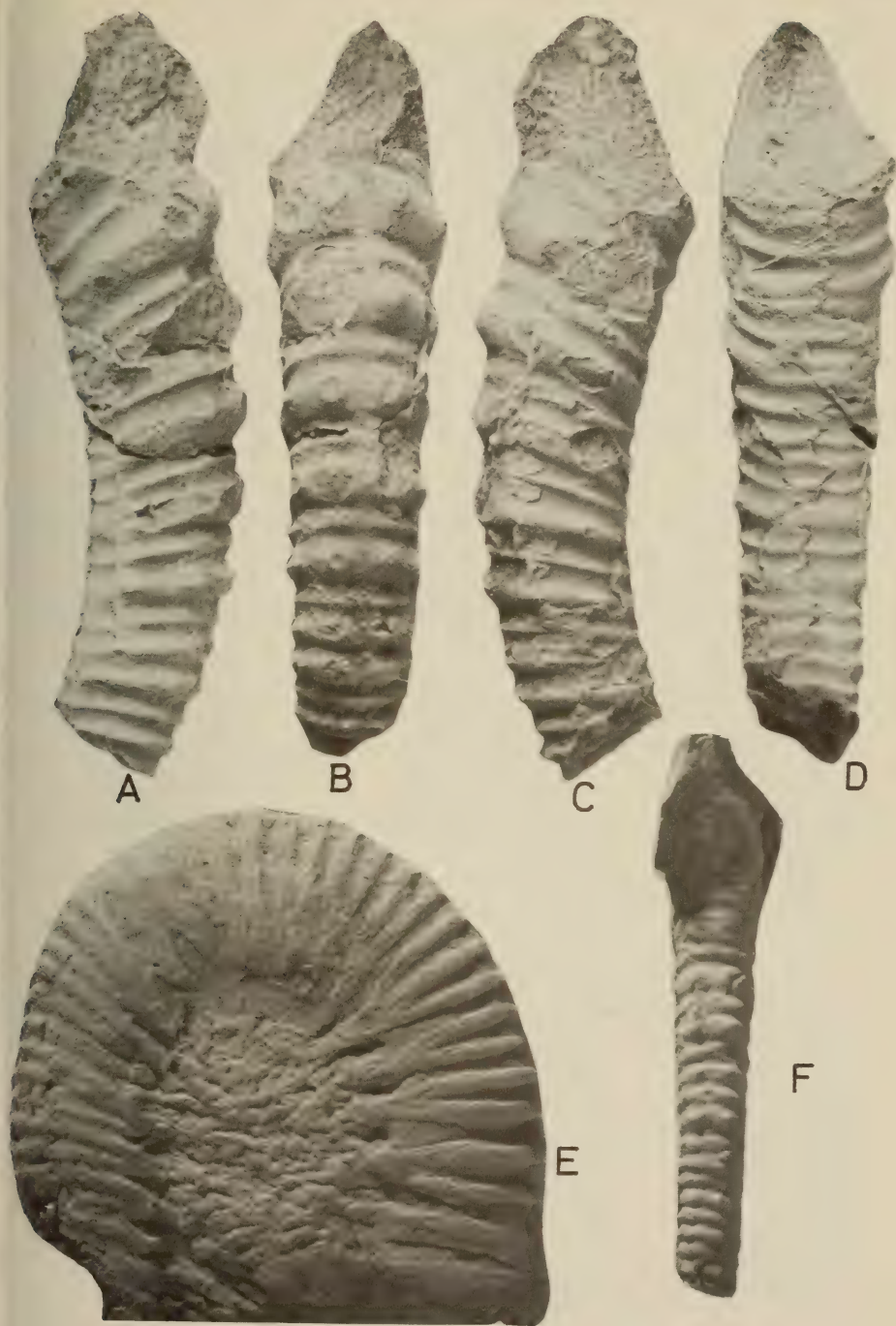


Fig. 59. A-D. *Toxoceratoides? haughtoni* sp. nov. BMNH C79701 from locality 166, Zululand, Aptian III.  $\times 2$ . E. *Toxoceratoides royerianus* (d'Orbigny, 1842). SAM-PCM5313 from Lubemba, Mozambique, Lower Aptian.  $\times 1,7$ . F. *Toxoceratoides krenkeli* Förster, 1975a. SAM-PCM5342 from Lubemba, Mozambique, Lower Aptian.  $\times 1,5$ .



*Material*

SAM-PCM5342 from Lubemba, southern Mozambique, Lower Aptian.

*Description and discussion*

A small, slightly curved part of the phragmocone is referred to Förster's species.

The whorl section is nearly circular on the earliest part preserved. Up to a diameter of 5,5 mm ornament consists of strongly prorsiradiate ribs, separated by interspaces of similar width. Rib density is about four per whorl height. The ribs weaken markedly on, and pass straight across the dorsum. Tuberculation commences at a diameter of 5,5 mm; at first only ventral tubercles are present, but four ribs further on, distinct, though small lateral and umbilical tubercles are present, and there are faint indications of duplication of ribs over the dorsum.

Förster (1975a: 160 *et seq.*) discussed the affinities of the species in detail; its main characteristic is the sparsity or absence of non-tuberculate intercalatories on the shaft. The present specimen adds to our knowledge of the species in that it illustrates that the early parts of the curved shaft lack tubercles; in this respect it resembles the later *Toxoceratoides? haughtoni* sp. nov. of Late Aptian age, described below.

*Occurrence*

Lower Aptian of southern Mozambique.

*Toxoceratoides? haughtoni* sp. nov.

Figs 59A–D, 60A–I, 61A–C, 62A–D, 63, 64A–C, 65A–B, 66B, 79A–B

*Holotype*

SAS 64/T1 from locality 168, Mfongozi Creek, northern Zululand. Aptian III–IV. South African Geological Survey Collection, Pretoria. Collected by H. Klinger 1970.

*Derivation of name*

The species is named in honour of Dr S. H. Haughton, discoverer of many Cretaceous localities in northern Zululand.

*Material*

Apart from the holotype, SAS L65/T2, SAS Z8/T1, SAS Z8/T4, SAS Z8/T5, SAS LJE 186, all from locality 168, Mfongozi Creek, Zululand, and BMNH C79690, C79191, C79694–79701 from locality 166, Aptian III, Aptian III–IV, and SAS N2 from locality 50.

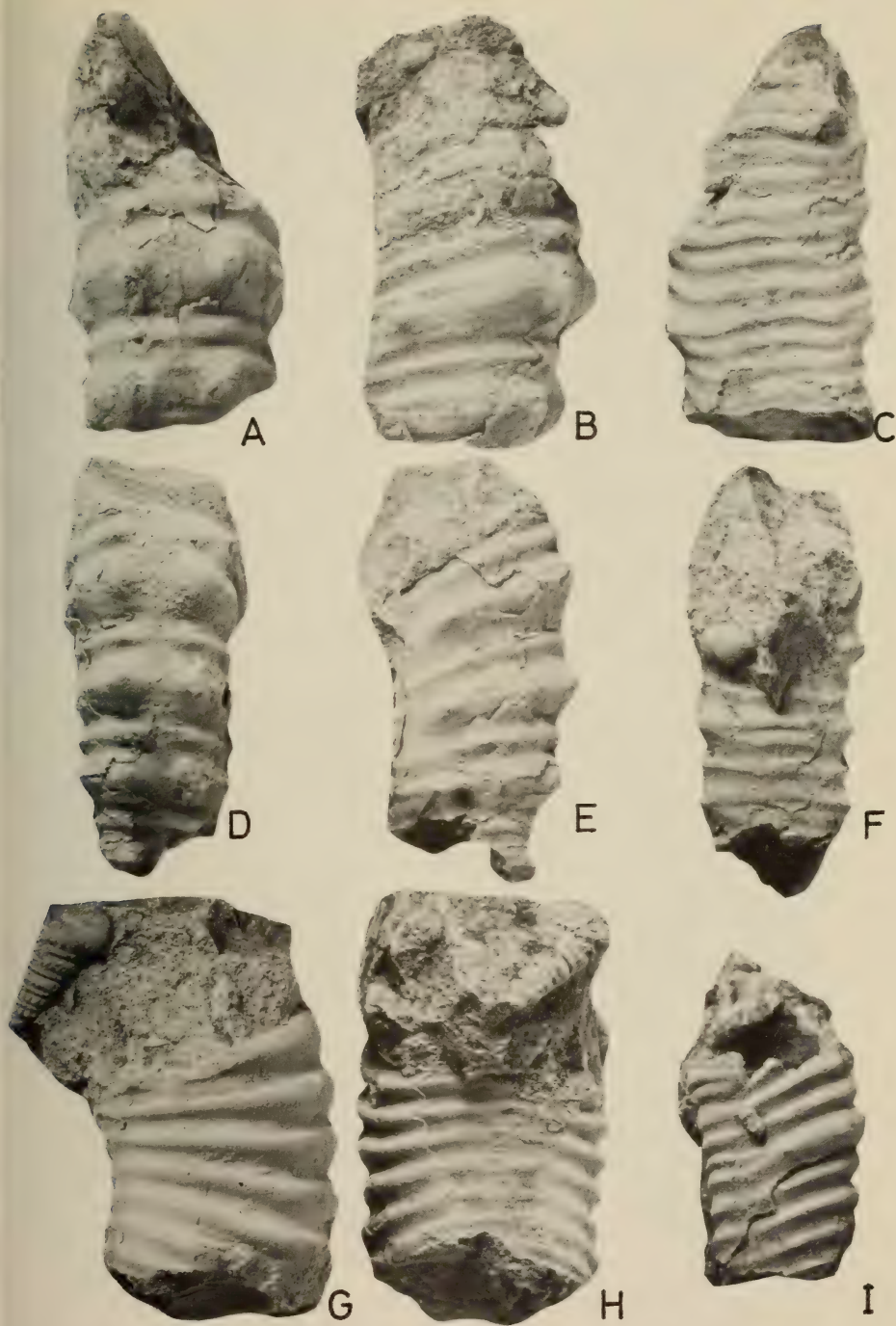


Fig. 60. *Toxoceratoides? haughtoni* sp. nov. A-C. BMNH C79695 from locality 166, Zululand, Aptian III. D-F. BMNH C79696, locality and age as above. G-I. BMNH C79712, locality and age as above. All  $\times 2$ .

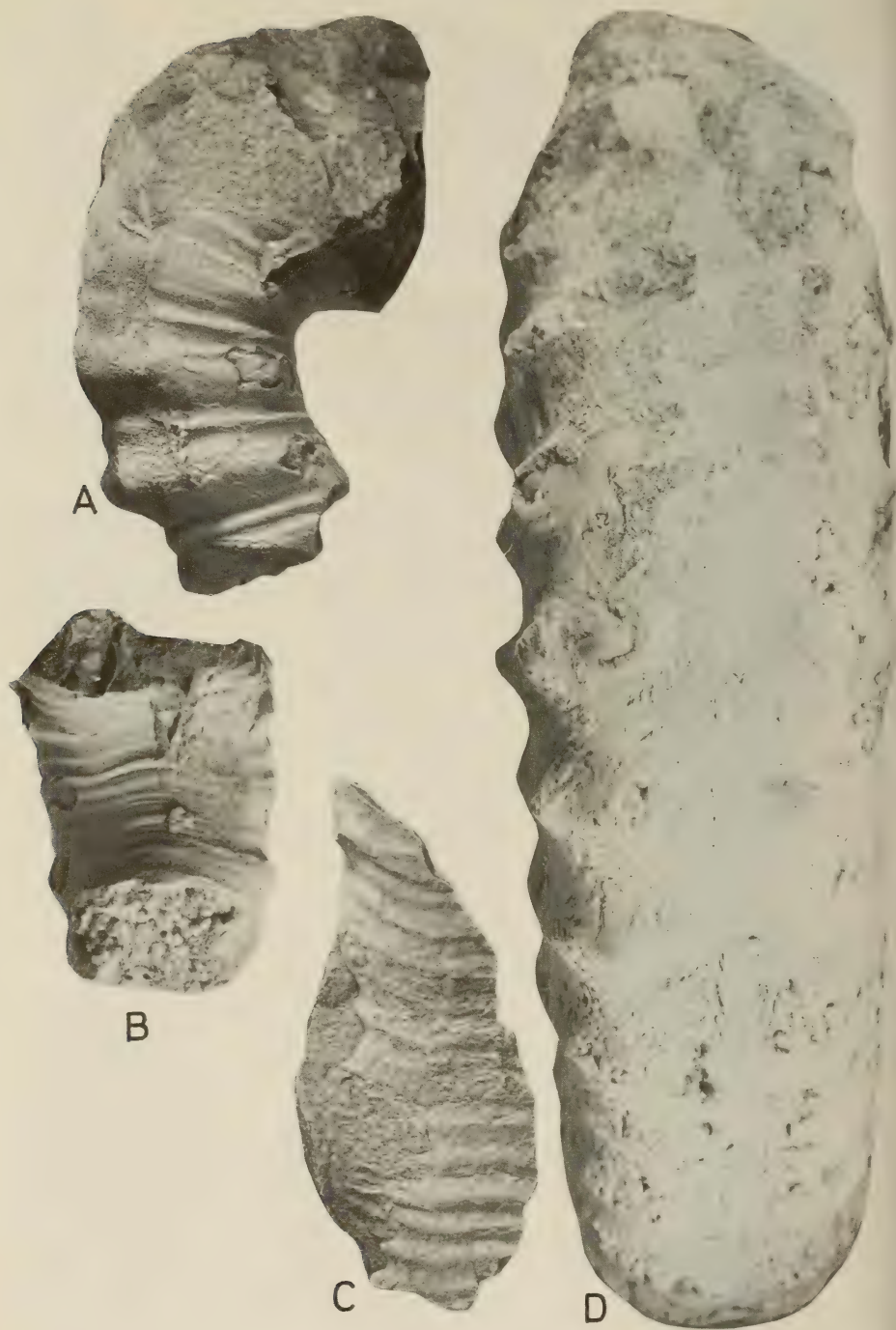


Fig. 61. A-C. *Toxoceratoides ? haughtoni* sp. nov. BMNH C79694 from locality 166, Zululand, Aptian III.  $\times 2$ . D. *Australiceras wandalina* (Boshoff MS) sp. nov. BMNH C7888 from locality 171, Zululand. Aptian.  $\times 0,67$ .



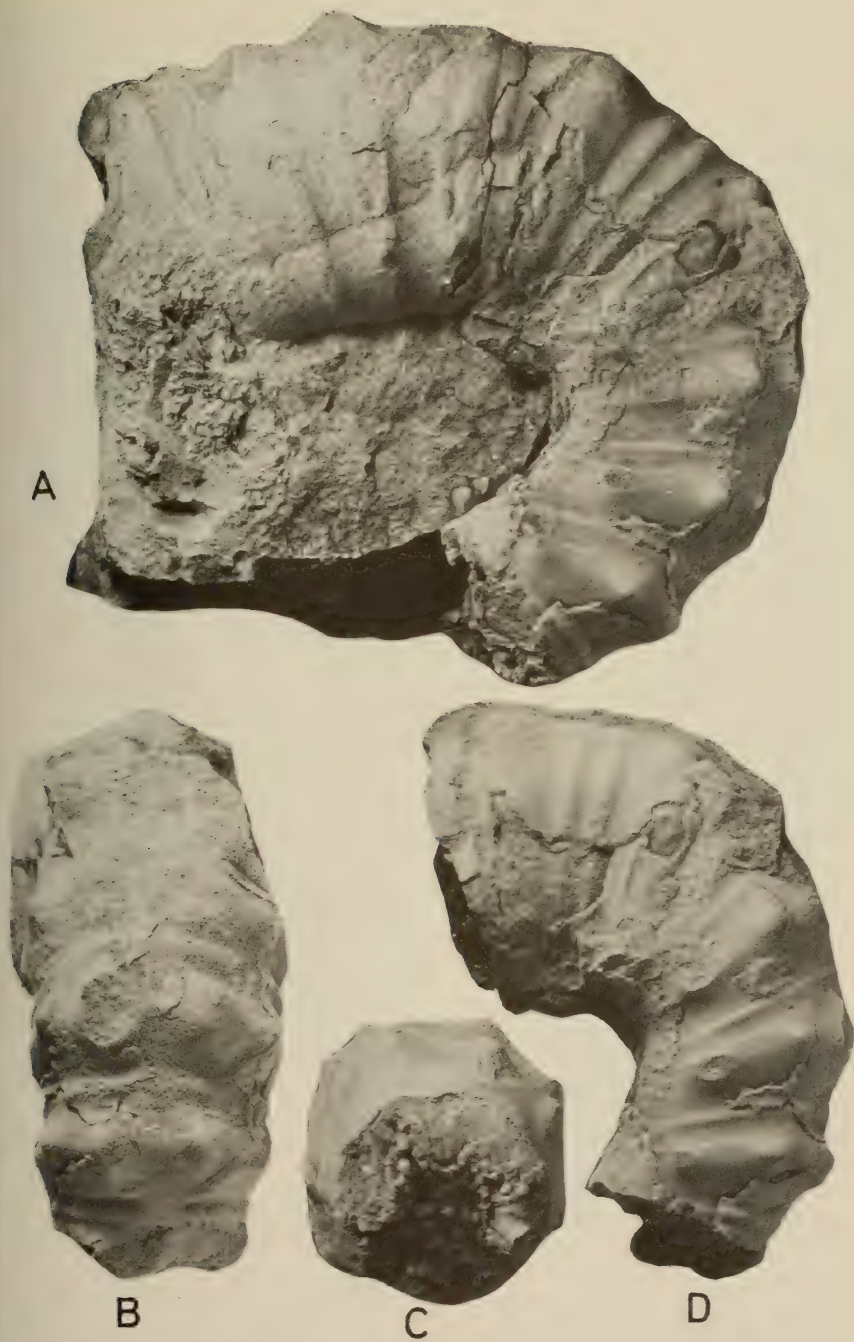


Fig. 62 A-D. *Toxoceratoides? haughtoni* sp. nov. BMNH C79694 from locality 166, Zululand, Aptian III.  $\times 2$ .

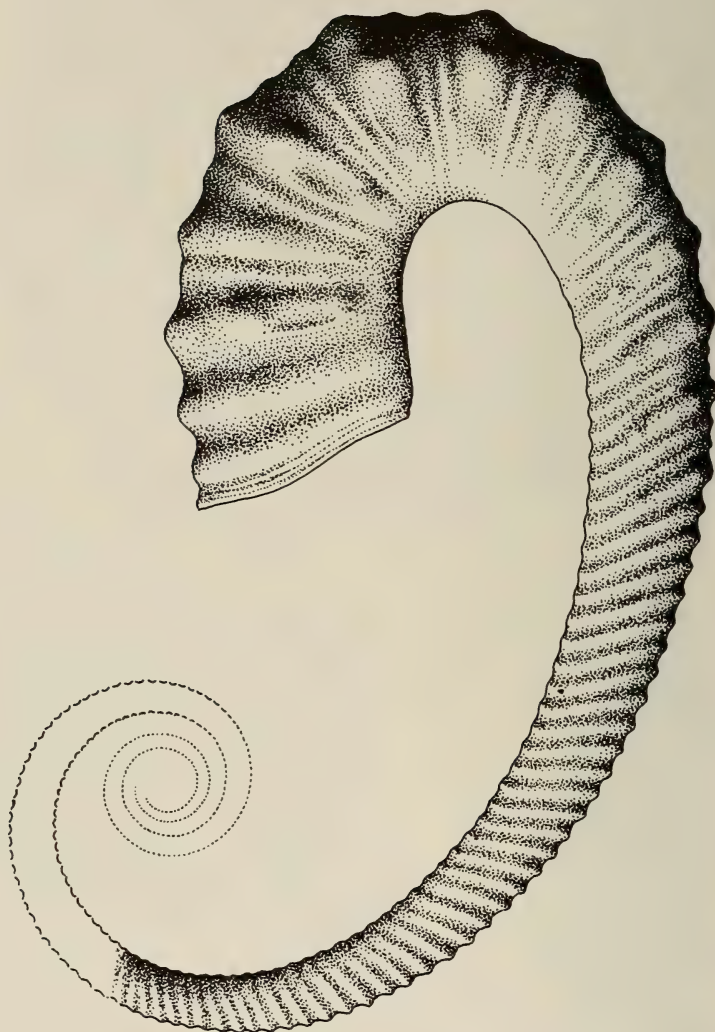


Fig. 63. Diagrammatic reconstruction of *Toxoceratoides? haughtoni* sp. nov.



Fig. 64. *Toxoceratoides? haughtoni* sp. nov. A. SAS Nd from locality 50, Upper Aptian.  $\times 1,6$ .  
B-C. SAS 64/T1, holotype from locality 168, Zululand, Aptian III-IV.  $\times 1,4$ .



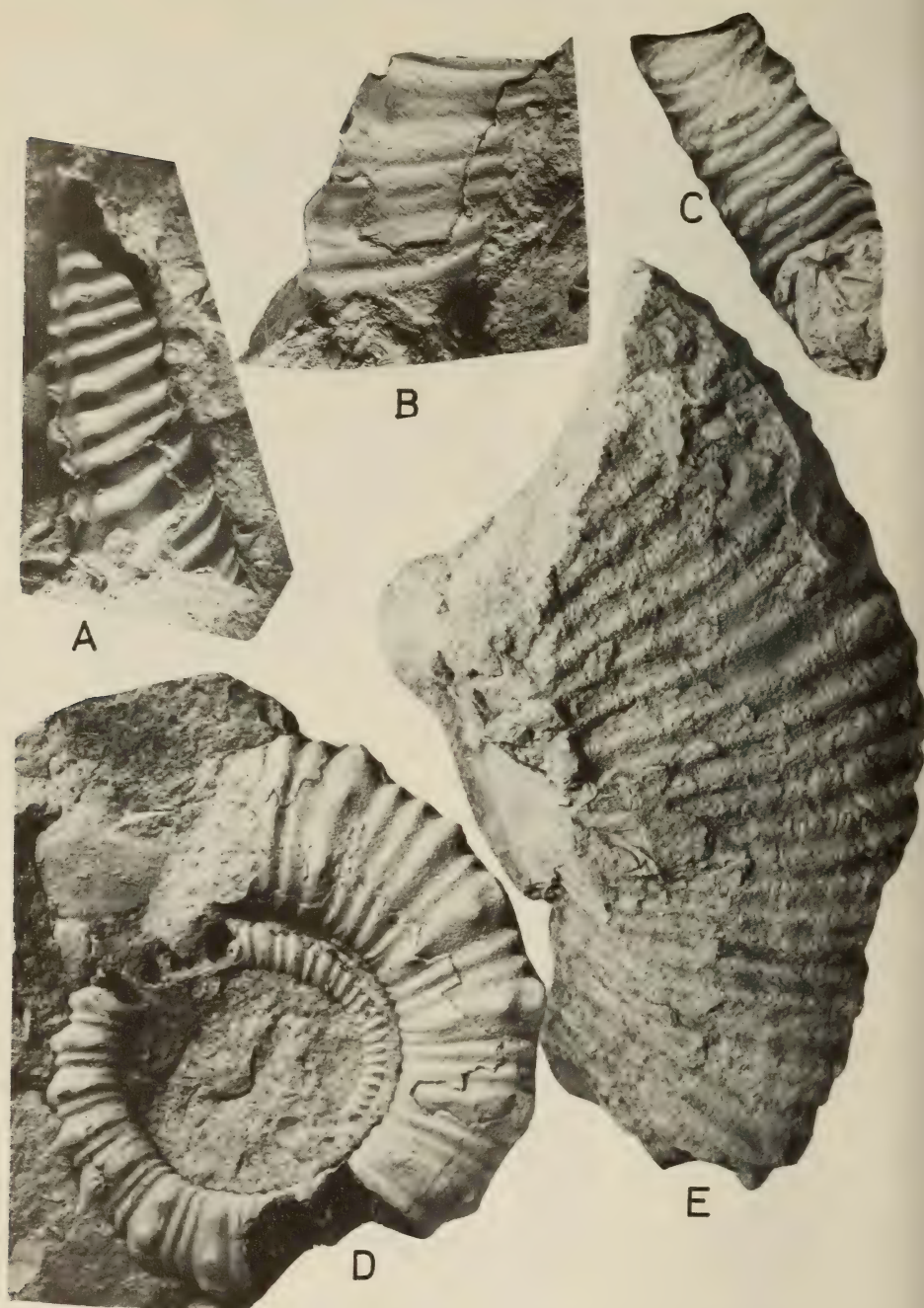


Fig. 65. A–B. *Toxoceratoides ? haughtoni* sp. nov. A. SAS LJE 186 from locality 168, Zululand, Aptian III–IV.  $\times 1,5$ . B. SAS Z8/T5 from locality 168, Zululand, Aptian III–IV.  $\times 1,5$ . C–D. *Australiceras* sp. aff. *irregulare*. C. SAS Z8/T5a from locality 168, Aptian III–IV.  $\times 1,5$ . D. SAS L65/2 from locality 168, Zululand, Aptian III–IV.  $\times 1$ . E. *Tropaeum obesum* sp. nov. SAM-PCZ5681. Fragment of inner whorl of holotype.  $\times 1$ .

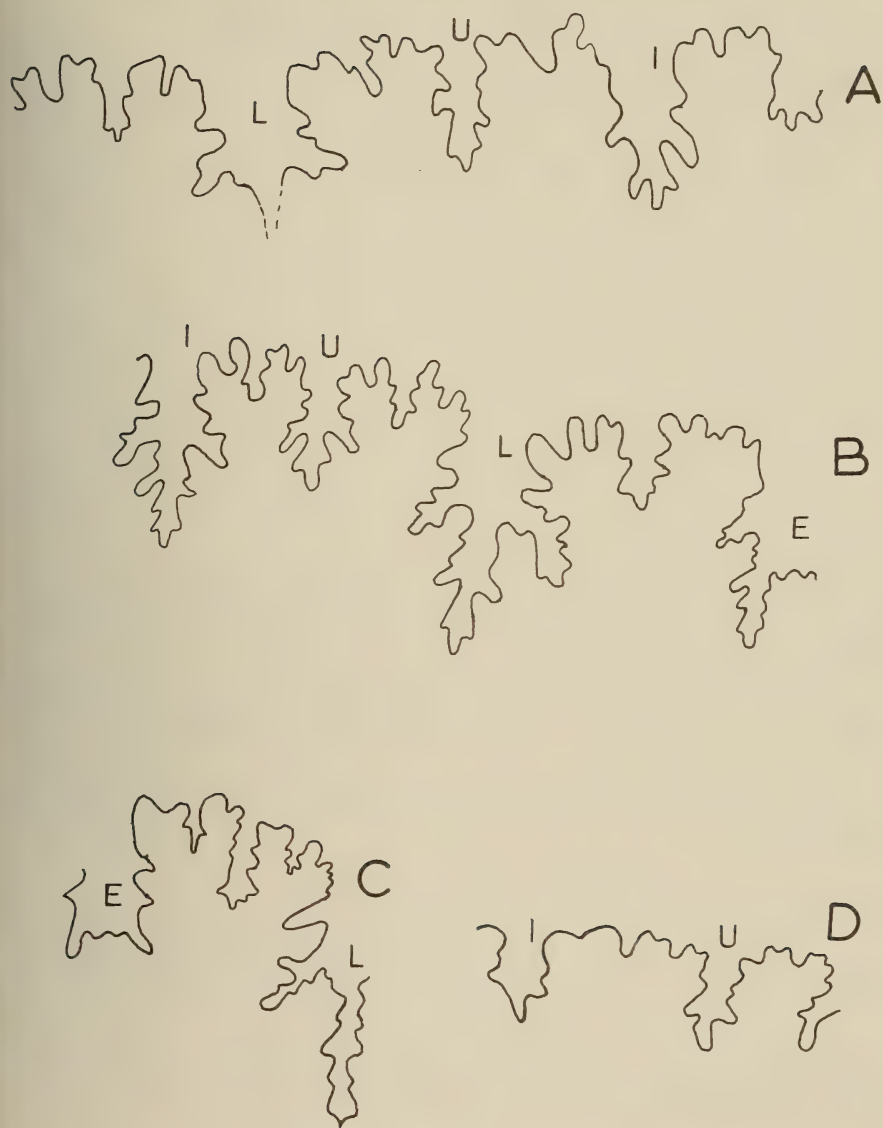


Fig. 66. A. Suture line of *Tonohamites koeneni* Casey, 1961. SAS Z1115 at diameter c. 8 mm.  $\times 6$ . B. Suture line of *Toxoceratoides? haughtoni* sp. nov. at diameter c. 8 mm.  $\times 6$ . C-D. Suture lines of *Tonohamites koeneni* Casey, 1961. C. SAS Z1115 at diameter c. 15 mm.  $\times 3$ . D. SAS H71D/19 at diameter c. 16 mm.  $\times 3$ .

*Description*

The coiling is toxoceratoid, open with a recurved crozier. The very early stage of growth is unknown. The whorl section is initially rounded, but becomes laterally compressed as size increases. Ornamentation is best shown by the holotype. At the smallest diameter, 6,1 mm, ornament consists of single, simple ribs, slightly prorsiradiate and separated by interspaces of similar width. At this stage there are approximately six ribs in a distance equal to the whorl diameter. At a slightly larger diameter the ribs become increasingly differentiated over the venter. Initially this appears as a mere flattening along the siphonal line, but at larger diameters the ribs are distinctly interrupted over the venter, terminating in small tubercles on either side of the siphonal line. Initially, all the tubercles are of equal size, but at a diameter of 8,5 mm some appear stronger than the others. With increasing diameter, these tubercles appear with greater frequency and become greatly enlarged, whilst the ribs on which they are situated become bolder on the flanks, and small ventrolateral and even smaller umbilical tubercles appear on the ventral and dorsal thirds of the flanks respectively. One (or rarely two) intermediate non-tuberculate ribs are present. At large diameters, the ribs connecting the ventral and ventro-lateral tubercles may become flattened, or even show signs of looping, in a manner reminiscent of some *Protanisoceras* species.

Ribbing weakens on the dorsum, and the ribs pass straight across or have a slight forward curvature. Some of the major ribs show distinct looping or duplication on the dorsum.

Ornament remains more or less constant up to the sharply recurved crozier. In the bend of the crozier more intercalated, thin ribs occur, and on the recurving limb all ornament, with the possible exception of the ventral tubercle, weakens.

The suture is relatively symmetrical with a trifid lateral, umbilical and internal lobe.

*Discussion*

All the available specimens show toxoceratoid coiling. If this species is a true *Toxoceratoidea*, it extends the range of the genus to the Upper Aptian. The peculiar ornament in the early whorls and the lack of regular simple ribbing in the crozier is different from that of the normal *Toxoceratoidea* ornament, hence the species is referred to this genus with doubt. This also serves to distinguish it from all the other known species of *Toxoceratoidea*.

The non-tuberculate ribbed stage is comparable to that of *T. krenkeli*. That species, however, is tuberculate at much smaller diameters and has a depressed whorl section, different from the compressed whorl of *T. ? haughtoni*.

*Ancylloceras patagonicum* Stolley (1912: 11, pl. 1 (figs 2a-b, 3a-b)) may also be compared with the present species. The Patagonian species has, however, stronger ribbing in the early stages of growth, whilst the major costae are not as strongly developed as in the present species.



One of Von Koenen's specimens of *Ancyloceras fustiforme* (1902, pl. 53 (fig. 9)) bears some resemblance to the early parts of *T. ? haughtoni* in having ventrally differentiated ribbing which becomes tuberculate with increasing diameter. In later stages, however, this species is not as strongly tuberculate as the Zululand material, as is illustrated by the original of Von Koenen's (pl. 41, fig. 9) specimen.

#### Occurrence

Fairly common in the Upper Aptian of Zululand.

#### Genus *Tonohamites* Spath, 1924

##### Type species

*Tonohamites decurrens* Spath, 1924 from the Lower Aptian of Ahaus, Germany, by original designation.

##### Diagnosis

Coiling labeceratid. Tuberculation weaker than in *Toxoceratoides* and mostly confined to the venter. Ribbing in early stages hamitid, but towards body chamber broad and flat in some.

##### Discussion

Like *Toxoceratoides*, *Tonohamites* was doubtfully regarded as a synonym of *Hamiticeras* by Wright (1957: L212). Casey (1961: 84), however, maintains that it is quite a valid and useful genus for small labeceratid-like forms with reduced tuberculation on the phragmocone and rounded ribbing on the venter. *Tonohamites decurrens* Spath with strong trituberculation on the phragmocone connects *Tonohamites* with *Toxoceratoides*, thus illustrating the close relationship between the two genera.

The genus was discussed at length by Casey (1961: 84) and, apart from extending the stratigraphic and geographical range of the genus, no further comments are necessary.

Species referred to *Tonohamites* by Casey are as follows:

1. *Tonohamites decurrens* Spath, 1924: 461. (Lectotype is Von Koenen's 1902, pl. 33 (fig. 2) and lower part of pl. 33 (fig. 3)).
2. *Tonohamites aequicingulatus* (von Koenen) (1902: 394, pl. 37 (figs 5a-c, 6a-e)).
3. *Tonohamites ? eichwaldi* (Jasykow) in Sinzow (1872: 36, pl. 6 (figs 7-9)).
4. *Tonohamites ? hunstantonensis* Casey (1961: 90, pl. 21 (fig. 1a-d)).
5. *Tonohamites koeneni* Casey: (1961: 89). Holotype is Von Koenen's (1902, pl. 33 (fig. 3a)) specimen, upper part only.
6. *Tonohamites limbatus* Casey (1961: 89, pl. 22 (figs 3a-c, 4), pl. 21 (fig. 3a-b)).
7. *Tonohamites ? undosus* (von Koenen) (1902: 393, pl. 35 (fig. 13a-f)).

##### Occurrence

*Tonohamites* occurs in the Lower Aptian of Europe and the Upper Aptian of Madagascar and Zululand.

*Tonohamites koeneni* Casey, 1961

Figs 66A, C-D, 67C-D, 73A, 81F

*Hamites decurrens* (non Roemer) von Koenen, 1902: 392, pl. 33 (fig. 3a upper part only).  
*Tonohamites koeneni*: Casey, 1961: 89, text-fig. 35g-h.

*Holotype*

The top part only of the specimen figured by Von Koenen (1902, pl. 33 (fig. 3)) as *Hamites decurrens* by original designation (Casey 1961: 89).

*Material*

SAS Z1115, SAS Z1118, SAS H71D/19 all from locality 152, Mkuze Game Reserve. Aptian IV.

*Description*

The most complete specimen, SAS Z1115 (Fig. 67C-D), shows the coiling to be labeceratid, with a moderately long shaft. Coiling of the very early whorls is unknown.

The whorl section is rounded in the early whorls, but becomes progressively flattened dorsoventrally with a nearly flat dorsum. Maximum width is at midflank or just dorsal to it. Ornament on the curved shaft consists of simple, prorsiradiate ribs, separated by narrower interspaces. The ribs are narrow on the dorsum and nearly radial, then are prorsiradiate and cross the flank with increasing strength. Towards the venter the ribs become more rounded and wider, a tendency which is especially pronounced on the body chamber. There are four to four and a half ribs in a distance equal to the whorl diameter on the shaft. At the bend on the crozier, the ribs become extremely flattened on the venter and the interspaces on the flanks become wider. The aperture appears to be quite simple, with neither lappets nor a constriction.

*Discussion*

As Casey (1961: 84) has outlined, Von Koenen's illustration of *Hamites decurrens* (1902, pl. 33 (figs 2, 3a-b)) is a synthetograph. The lower part of the synthetograph was chosen by Casey as lectotype of *Tonohamites decurrens* Spath, whilst the upper part was regarded as a new species, *Tonohamites koeneni*. The Zululand material fits the upper part of Von Koenen's figure so well that the authors have no hesitation in referring it to *T. koeneni*, despite differences in age. *T. koeneni* is believed to be of Lower Aptian age (as is the whole genus in the sense used by Casey (1961: 85)). The Zululand material is of Upper Aptian age, occurring just below the line of hiatus concretions (Kennedy & Klinger 1972) marking the Aptian/Albian boundary.

Casey's *Tonohamites* cf. *koeneni* (1961: 89, pl. 20 (fig. 5a-b)) from the Lower Aptian of Kent does not show as pronounced broad flattened ribs on the body chamber as do Von Koenen's or the Zululand specimens.

*Tonohamites decurrens* Spath has a distinct trituberculate phragmocone,

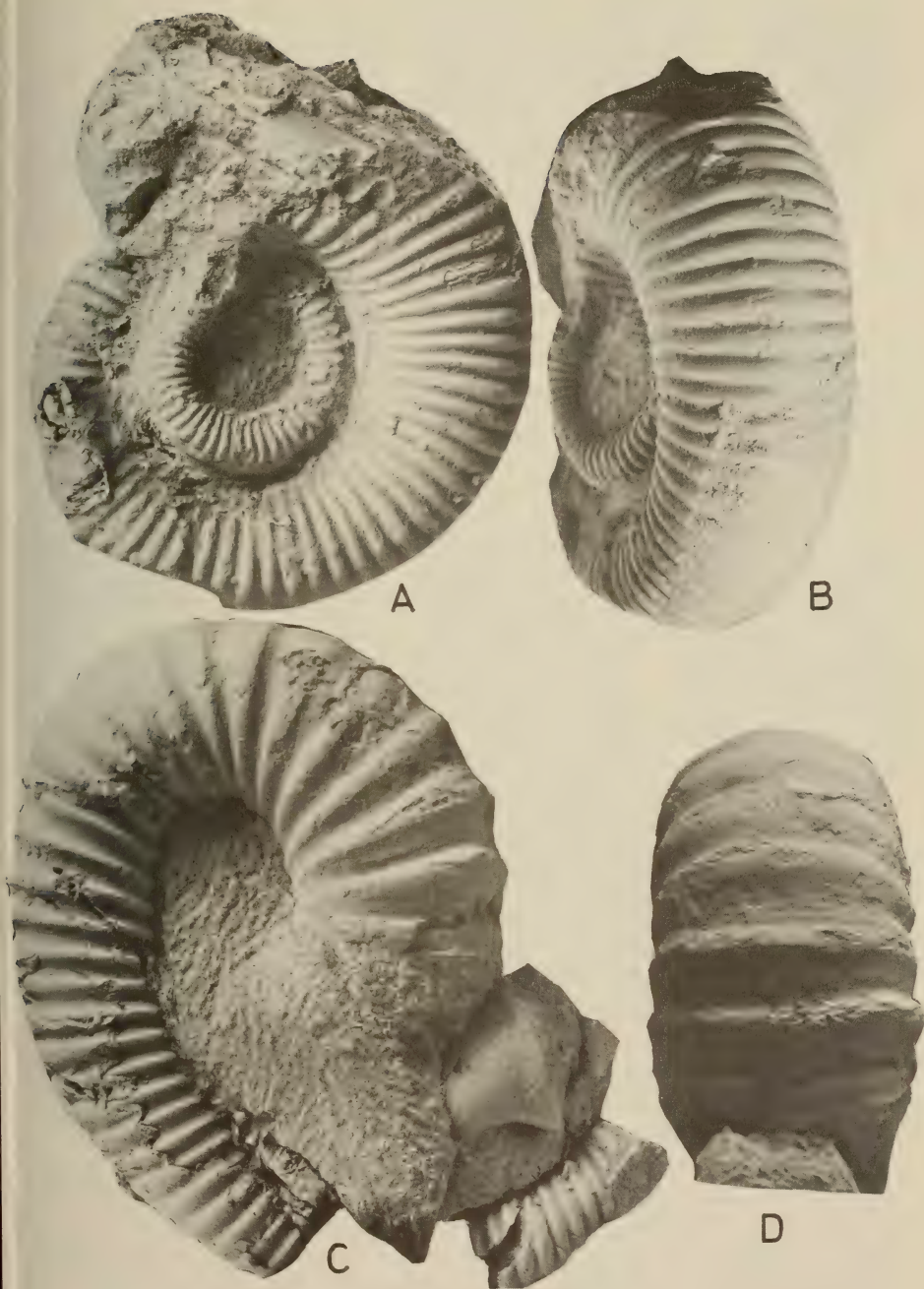


Fig. 67. A-B. *Helicancyloceras (Helicancyloceras) densecostatum* sp. nov. SAM-PCZ5682, holotype from locality 168, Zululand, Aptian III-IV.  $\times 1,3$ . C-D. *Tonohamites koeneni* Casey, 1961. SAS Z1115 from locality 152, Zululand, Aptian IV.  $\times 1,4$ .



and is easily distinguished. *T. aequicingulatus* (von Koenen) has a somewhat similar body chamber, but has ventral tubercles on the shaft. *T. limbatus* Casey has a long, descending limb and small tubercles on the phragmocone.

#### Occurrence

Upper Aptian of Zululand. The English specimen tentatively referred to the species by Casey is from the Lower Aptian *bowerbanki* Zone. In Germany the species occurs in the Lower Aptian of Ahaus.

#### *Tonohamites aequicingulatus* (von Koenen, 1902)

Figs 68A–E, 38C, 88D

*Hamites aequicingulatus* von Koenen, 1902: 394, pl. 37 (figs 5–6).

*Tonohamites aequicingulatus* Casey, 1961: 87, pl. 9 (figs 2a–b, 3a–b, 4), text-fig. 32.

*Tonohamites* sp. aff. *aequicingulatus* Collignon, 1962: 14, pl. 221, (fig. 970).

#### Lectotype

The original of Von Koenen (1902, pl. 37 (fig. 5a–c)) by subsequent designation Casey 1961: 87.

#### Material

SAS Z8Ta1 from locality 168, BMNH C79690, C79692 from locality 166, Mfongozi Creek, Zululand. Aptian III–IV.

#### Description

The available specimens are fragmentary and consist of slightly curved shafts. The whorl section is depressed, with rounded flanks and a flattened dorsum and venter.

Ornament consists of prominent, obliquely prorsiradiate ribs, separated by wider interspaces. The ribs are strongest on the flanks, thickening towards the ventrolateral region. In the siphonal area the ribs are interrupted or weakened at the larger diameter. At the smaller ends of the shaft there is no distinct weakening of ribbing over the venter. The ribs pass radially or with a slight forward curvature over the dorsum.

#### Discussion

*T. aequicingulatus* presents difficulties in interpretation, as it is only known from fragments, and, as Casey (1961: 88) noted, it 'seems practicable to treat these fragments as belonging to a single, variable species'.

The Madagascan specimen tentatively referred to this species by Collignon has a rib density of four or five per diameter, the general appearance being similar to that of the Zululand material, and it is probably conspecific. The only apparent difference between the figured European specimens in Casey (1961) and Von Koenen (1902) and those from Zululand and Madagascar, is that the ribbing in the latter specimens is stouter near the venter. The subsymmetrical

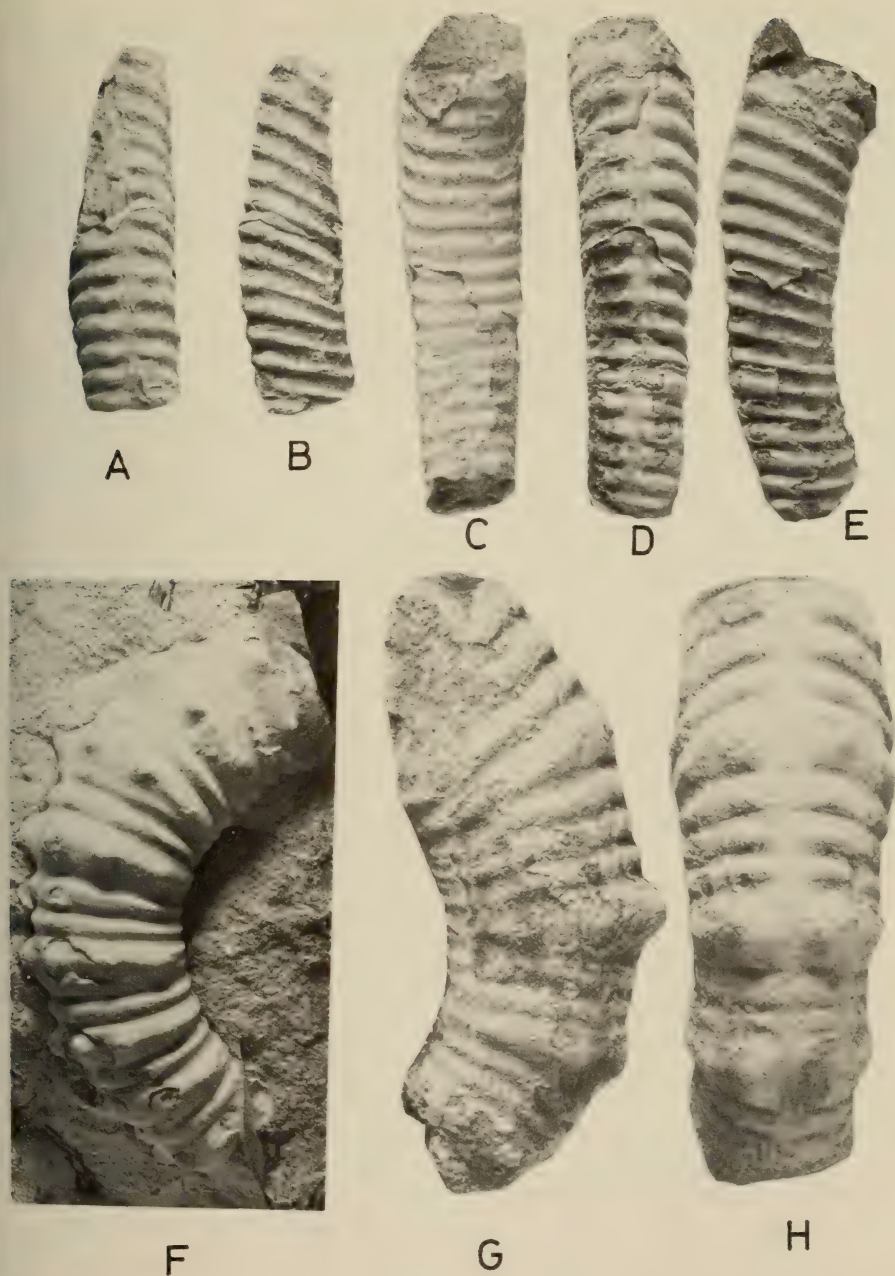


Fig. 68. A-E. *Tonohamites aequicingulatus* (von Koenen, 1902). A-B. BMNH C79692 from locality 166, Zululand, Aptian III.  $\times 2$ . C-E. BMNH C79690 locality and age as above.  $\times 2$ . F. *Australiceras* sp. aff. *A. irregulare* (Tenison Woods). BMNH C79714 from locality 167, Zululand, Aptian III-IV.  $\times 1$ . G-H. *Helicancyloceras* (*Nonyaniceras*) sp. indet. BMNH 79717 from locality 167, Zululand, Aptian III-IV.  $\times 2$ .

lateral lobe mentioned by Casey (1961: 88) is noticeable in both the Zululand and the Madagascan material.

#### *Occurrence*

*Tonohamites aequicingulatus* occurs in the Lower Aptian *bowerbanki* subzone in England. Von Koenen (1902: 394) referred his specimens to the Aptian and with a question mark to the Zone of *Hoplites deshayesi*. The Madagascan specimen is from the Upper Aptian Zone of *Aconeceras nisus* and *Melchiorites melchioris*.

#### *Tonohamites? caseyi* sp. nov.

Fig. 69 (see also Fig. 46)

#### *Holotype*

SAS Z804, the specimen marked A from locality 150 or 151, Mkuze Game Reserve. Aptian IV. Geological Survey Collection. Collected by the late Dr E. C. N. van Hoepen.

#### *Derivation of name*

Named after Dr R. Casey, Institute of Geological Sciences, London.

#### *Description*

Eleven fragments of a heteromorph with labeceratid coiling were partially exposed by preparation from the body chamber of the large *Tropaeum* described above (p. 285).

The holotype shows that coiling is very similar to that of *Tonohamites koeneni* with the early part protruding beyond the venter of the aperture. Ribbing on the early parts is only partially known, and appears to have been strongly rounded and annular. Towards the crozier ribbing becomes more prominent, and the ribs appear to arise at the umbilical edge, are slightly sinusoidal across the flanks, and become progressively wider towards the venter. Over the venter the ribs are broad and elevated, with high-walled interspaces. Occasional bifurcations occur. The suture line is unknown.

#### *Discussion*

Initially only part of one specimen was exposed at the venter of the body chamber of the *Tropaeum* sp. After preparation, parts of ten more were found, but due to the hardness of the matrix much of the detail of the specimens has been destroyed.

The labeceratid coiling, and the apparent absence of tuberculation are the most obvious *Tonohamites*-like characteristics. The very striking broad, high-crested ribs on the body chamber are very much like those found in hamitids of the *Hamites gibbosus* type, and point to allocation to *Helicancylus* in the sense of Casey (1961: 85), confirming once more the close relationship between the



various helicancylid genera, and the perhaps doubtful validity of retaining *Toxoceratoides*, *Tonohamites* and *Helicancyclus* separate.

None of the other Aptian heteromorphs from Zululand has the high-crested crozier ribbing of *T. ? caseyi*; neither has any of the *Tonohamites* or toxoceratoid species described by Casey (1960).

#### Occurrence

Upper Aptian of Zululand.

#### Subfamily Heteroceratinae Spath, 1922

Heteromorphs with an initial helix or open spire, followed by planispirally coiled whorls, a curved or straight shaft and recurved crozier are referred to the Heteroceratinae.

Apart from the fact that the group is in need of restudy in the classical European localities, there are some nomenclatorial difficulties, one of which will be discussed below.

A perusal of the literature shows that authorship of the Heteroceratinae (or -dae) is ascribed to either Hyatt 1900 (see Wright 1957: L212; Drushchitz & Kudryavtzev 1960: 296; Dimitrova 1967: 64; Thomel 1964: 62; Vašičec 1972: 57, etc.) or to Spath 1922 (see Luppov & Drushchitz 1958: 105; Egojan 1965: 117; Dimitrova 1970: 94; Kakabadze 1971a: 109, 1971b: 39, etc.). In the English version of *Zittel's Textbook of Palaeontology* published in 1900, Hyatt, however, never mentioned Heteroceratidae. He included *Hamites* Parkinson, 1811, *Hemibaculites* Hyatt, 1900, *Dirrymoceras* Hyatt, 1900 and *Torneutoceras* Hyatt, 1900, in the Hamitidae, and added 'here should also be placed *Helicoceras* and *Heteroceras* d'Orb., and *Lindigia*, Karstens . . .'. Spath stated (1922: 148) that '*Heteroceras*, *Hemibaculites*, *Dirrymoceras* and *Lindigia* may be united as Heteroceratinae', and from this it should be clear that authorship is referable to Spath (1922) and not to Hyatt (1900).

Some of the most recent comprehensive publications on Heteroceratinae, especially the colchiditids, are by Kotetitchvili (1970) and Kakabadze (1971a, 1971b).

To the Heteroceratinae may be added *Helicancyloceras* gen. nov. (type species *Heteroceras* (*Argvethites*?) *vohimaranitraensis* Collignon, 1962) from the Upper Aptian of Madagascar and possibly *Kutatissites* Kakabadze, 1970. The subfamily Heteroceratinae is otherwise represented in the Barremian of Zululand by *Heteroceras* sp. *Colchidites* gr. ex. *colchicus* spp., *Colchidites* sp. indet. and *Paraimerites* sp. These species, and a detailed discussion on the Heteroceratinae are given elsewhere (Klinger 1976).

#### *Helicancyloceras* gen. nov.

##### Type species

*Heteroceras* (*Argvethites*?) *vohimaranitraensis* Collignon (1962, pl. 14, pl. 221 (fig. 962), from the Upper Aptian of Madagascar.



Fig. 69. *Tonohamites? caseyi* sp. nov. SAS Z804 from locality 151, Zululand, Aptian IV. Photograph of cast of original, arrow indicates holotype.  $\times 0,65$ .

#### *Diagnosis*

In typical forms, early whorls coiled in a shallow helix; later whorls may be coiled planispirally in same plane as helix. Size varies considerably, and early species may possibly be more loosely coiled. Ornament consists of ribbing with or without two to three rows of tubercles on each side. Tubercles, if present, become weaker or disappear at varying stages. Lateral, umbilical and internal lobe trifold. Saddles bifid. Age: Upper Aptian.

*Helicancyloceras* (*Helicancyloceras*) subgen. nov.*Diagnosis*

Ribbing interrupted over venter in early whorls and ribs may end in small tubercles on either side of the siphonal line. Adult ornament consists of non-tuberculate ribs. Ribs may be flattened over venter with slight forward curvature nearly touching each other, creating 'paternoster' beaded effect.

*Helicancyloceras* (*Nonyaniceras*) subgen. nov.*Type species*

*Helicancyloceras* (*Nonyaniceras*) *nonyani* sp. nov.

*Diagnosis*

Planispiral coiling is attained rapidly. Early whorls with either ventral or ventral and lateral rows of tubercles on every rib. With increasing diameter intermediary non-tuberculate ribs occur. Tuberculate ribs may be stronger than intermediaries. Umbilical tubercles, if present, very weak. Tuberculation may disappear or become modified at various stages.

*Discussion*

Abundant fragments of this heteromorph genus occur in the Upper Aptian of Zululand in the Mkuze Game Reserve and along the Mfongozi Creek. Due to the general fragmentary nature of the material, only a few well-defined species may be recognized. The rest of the material is either mentioned or described without specific reference.

The majority of specimens consists of small helices only. Fortunately one specimen (Figs 70–71) shows remains of helical inner whorls, followed by a massive planispiral phragmocone and parts of the body chamber. The authors were at first inclined to regard the helically coiled forms as the ancestors of the larger forms with planispiral outer whorls. Detailed collecting, however, showed that both forms can occur at the same stratigraphic level. Whether the two size groups represent juvenile and adult stages respectively or sexual dimorphs is not known. The predominance of small helices may be due to selective postmortal transport, and may not reflect the true character of the population. In general, however, specimens with well-developed helices dominate at lower stratigraphic levels whereas forms with very shallow helices appear to be younger.

The affinities of the genus are enigmatic. At first glance the helical coils recall the Middle Albian hamitids once referred to d'Orbigny's genus *Helicoceras*. These, however, are true hamitids with a bifid lateral lobe. The helical coiling in *Helicancyloceras* points strongly to the Heteroceratinae, whilst the tuberculate species show ancyloceratine or perhaps helicancyline affinities. As has been pointed out earlier, the subfamilies are primarily accepted because they feature a certain degree of morphological homogeneity. Reference of *Helicancyloceras* to the Heteroceratinae rather than the Ancyloceratinae or Helicancylinae is thus based entirely on morphological criteria.



None of the heteroceratids appears suitable as an ancestral form, mainly because of the time gap between them and *Helicancyloceras*. The heteroceratids with the possible exception of the dubious *Hemibaculites* Hyatt, 1900, are restricted to the Barremian. Nevertheless, the relationship of *H. (Helicancyloceras)* to *H. (Nonyaniceras)* is similar to that of *H. (Heteroceras)* to *H. (Argvethites)* or of *Colchidites* to *Imerites*.

The very enigmatic genus *Kutatissites* Kakabadze, 1970 (type species *K. bifurcatus* Kakabadze, 1970), thus far known only from the Late Barremian of Georgia (U.S.S.R.) and France is another helically coiled form which may be considered ancestral. Thieuloy (1976) provides an extensive description of the French representative of this species, *K. edwardsi* (Reynes, 1876) and tentatively refers the genus to the Helicancylinae. Again the difference in age (late Barremian vs late Aptian) seems to stand in the way of deriving *Helicancyloceras* directly from *Kutatissites*.

Representatives of the Ancyloceratinae may provide the answer. *Helicancyloceras* could possibly be derived from an australiceratid such as *Australiceras irregulare* (Tenison Woods) with irregular early whorls not lying in one plane (see Day 1974, pl. 2 (Fig. 3)). *Australiceras* loses tuberculation in the middle stages of life. In the hypothetical ancestor of *Helicancyloceras* (*Helicancyloceras*), reduction of tuberculation could have affected the early whorls already, whereas the reduction in *H. (Nonyaniceras)* could have been retarded. In this case the relationship of *H. (Helicancyloceras)* to *H. (Nonyaniceras)* would be somewhat analogous to that of *Tropaeum* to *Australiceras* as far as the presence or absence of tubercles is concerned.

Whatever the origin of *Helicancyloceras* may be, the ornamentation and mode of coiling combines features of Ancyloceratinae, Helicancylinae and Heteroceratinae, again pointing to the rather artificial status of these groups. Reference of *Helicancyloceras* to the Heteroceratinae is done for pure morphological reasons, in full cognizance that this might imply a diphyletic origin for the Heteroceratinae (if they are to be retained as a separate group).

Furthermore, *Helicancyloceras* illustrates another attempt towards recoiling, and thus, (presumably) a more active mode of life for the animals concerned.

*Helicancyloceras (Helicancyloceras) vohimaranitraensis*

(Collignon, 1962)

Figs 70, 71A-B, 73B, D, 74A-F, 75B-C, E-G, 76A-B?, 77D-E, ? F-G, 78C, 88A-C

*Heteroceras (Argvethites?) vohimaranitraensis* Collignon 1962: 14, pl. 221 (fig. 962). Klinger 1976: 14, pl. 1 (nos. 3-5), figs 5d-e, 6b-e.

*Holotype*

Collignon's (1962, pl. 221 (fig. 962)) specimen from the Upper Aptian of Betioky, Madagascar.



Fig. 70. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). SAS H71D from locality 152, Mkuze Game Reserve, Zululand, Aptian IV. Largest available specimen with helicoid inner whorl, but completely symmetrical planispirally-coiled outer whorl.  $\times 0,86$ . (See also Fig. 71.) Possible sexual dimorph?





Fig. 71. A-B. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). SAS H71D from locality 152, Mkuze Game Reserve, Zululand, Aptian IV. Note the helical inner whorl.  $\times 0,75$ .



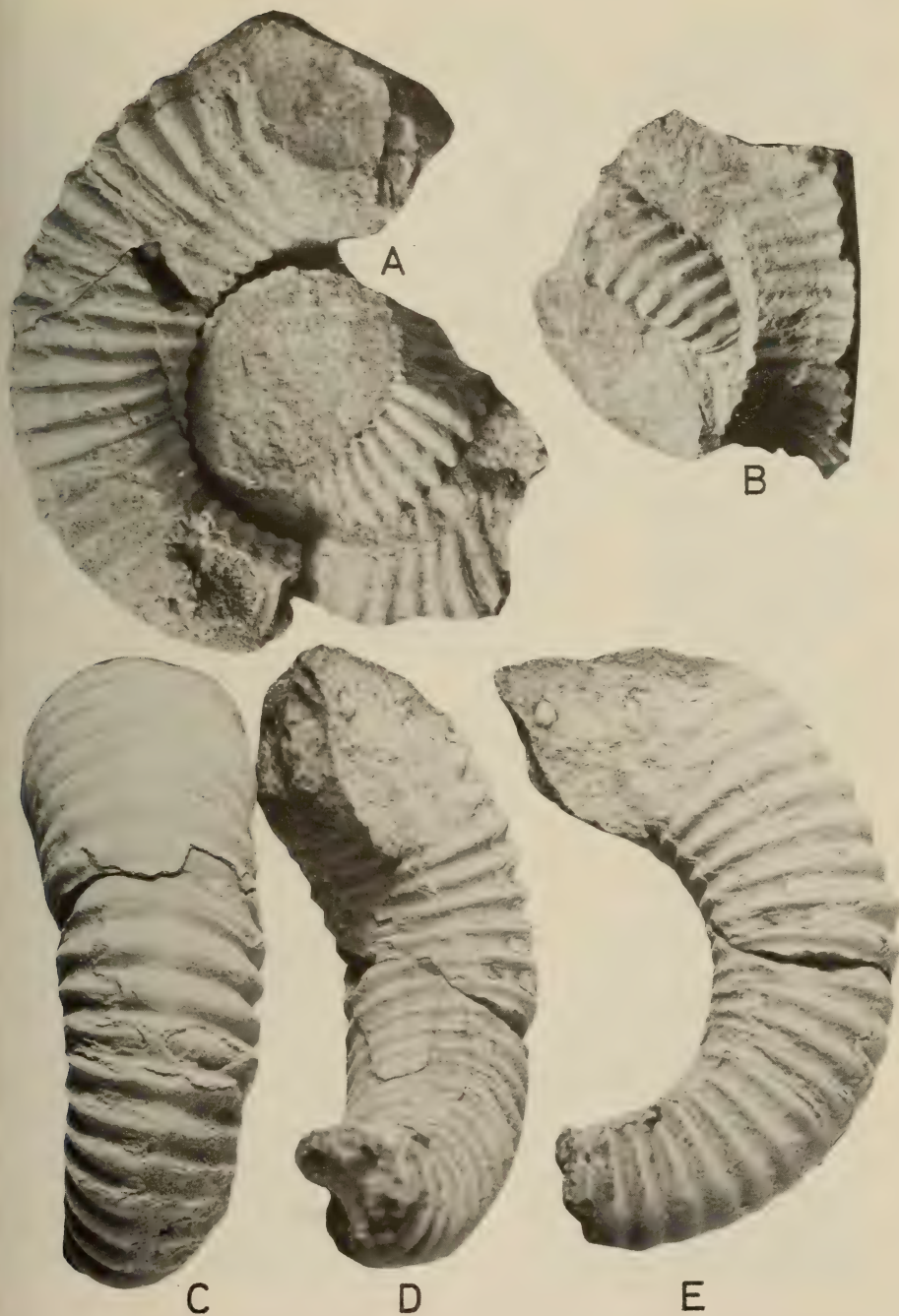


Fig. 72. A-E. *Helicancyloceras* (*Nonyaniceras*) *circulare* sp. nov. BMNH C79718 from locality 166, Zululand, Aptian III.  $\times 2$ .



Fig. 73. A. *Tonohamites koeneni* Casey, 1961. SAS Z1115 from locality 152, Zululand, Aptian IV.  $\times 1,3$ . B, D. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitarenensis* (Collignon, 1962). SAS Z9(5) from locality 168, Zululand, Aptian III-IV. This is an extremely coarsely ribbed specimen.  $\times 1,6$ . C. *Helicancyloceras* (*Helicancyloceras*) sp. indet.  $\times 1,5$ .



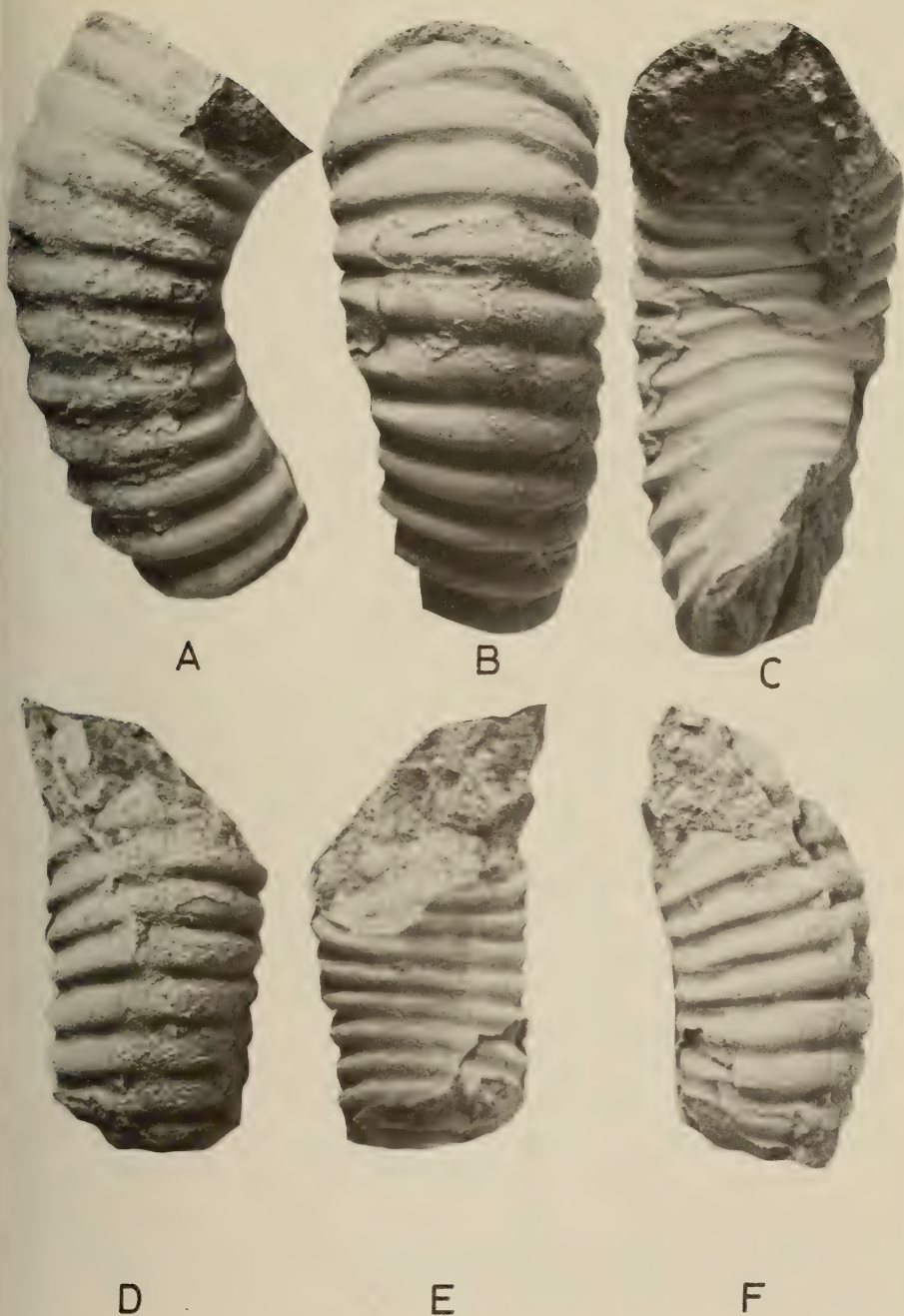


Fig. 74. A-F. *Helicancyloceras (Helicancyloceras) vohimaranitraensis* (Collignon, 1962).  
 A-C. BMNH C74709 from locality 166, Zululand, Aptian III.  $\times 2$ . D-F. BMNH C79711,  
 same locality and age as above.  $\times 2$ .



*Material*

SAS Z8(6), SAS Z8/3, SAS 871D/12, SAS H71D, SAS Z1153, all from locality 168 and 152. Aptian III-IV: BMNH C79703-C79712, all from locality 166, Aptian III.

*Description*

Early stages of growth are helical, either dextral or sinistral, consisting of about one and a half to two whorls. The distance between the successive whorls is extremely variable. After the helical stage coiling becomes planispiral in some specimens.

Ornament in the helix consists of prominent ribs, narrowest and least prominent on the dorsum, wedge-shaped on the flanks and broadest over the venter. Interspaces on the flanks are about as wide as the ribs. Ribbing over the venter is very variable. At small diameters the ribs are interrupted or weakened on the venter, in some cases forming small pimple-like tubercles on either side of the siphonal line. At large diameters the ribs cross the venter with a slight forward curvature and a thickening in the interspaces, thus forming a 'pater-noster' effect. In the planispiral part of the shell the ribbing becomes finer and wider-spaced and somewhat rursiradiate. Ribbing over the dorsum is very weak at this stage. Occasional bifurcations occur at the umbilical edge. On the body chamber the whorl section becomes dome-shaped with a flattened dorsum and broadly inflated flanks and venter. The suture line is relatively simple with bifid saddles and trifid L, U, I lobes. L is largest and U smallest.

*Dimensions*

<i>Specimen</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>H</i> (height of spire)
H71D	175	64(36,7)	76(44,7)	0,84	64(36,5)	—
SAS Z9(5)	46	14(30,4)	12(26)	1,17	22(47,8)	23

*Discussion*

As can be seen from the figures, the species is interpreted rather widely, and is intimately connected to *H. (H) densecostatum* sp. nov. by finer-ribbed specimens such as BMNH C79713 (Fig. 75B-C), SAS Z8/Hd (Fig. 76B) and SAS A1294 (Fig. 79C). It is similarly connected to *H. (N.) circulare* from which it differs in becoming planispiral at later stages and in lacking regular tuberculation in the early stages of growth.

The occurrence of both large and small forms at the same stratigraphic level (e.g. SAS H71D and SAS H71D/12, Figs 70, 71A-B, 76A) is of interest; sexual dimorphism seems the most likely explanation. The helical inner whorls of the large specimen SAS H71D are indistinguishable from isolated helices or fragments of helices, indicating conspecificity, and, that in some cases at least, the shell changes to a planispiral mode of coiling after an initial helical stage.

The inner whorls are easily distinguished from other heteromorphs occurring at this stratigraphic level by the helical coiling and curious mode of ornament over the venter. Small fragments bear similarity to the inner whorls of *Tropaeum*, but are distinguished by the oblique ribbing. Small pieces of *Tonohamites koeneni*, which occur at the same level, are distinguished by the same character.

The outer, planispiral whorls, with symmetrical ribbing are easily mistaken for *Tropaeum* or *Australiceras*, and, unless associated with the inner whorls, may be indistinguishable.

#### Occurrence

The species occurs in the Upper Aptian zone of *Epicheloniceras tschernischewi* of Madagascar, and Aptian III-IV of Zululand.

#### *Helicancyloceras (Helicancyloceras) densecostatum* sp. nov.

Figs 67A-B, 75B-C?, I-J, 76B?, 79C, 81D

*Heteroceras (Argvethites?) vohimaranitraensis* Klinger, 1976: 14 (pars), pl. 2 (no. 5) only.

#### Holotype

SAM-PCZ5682 from locality 168 Mfongozi Creek, Zululand. Aptian III-IV. South African Museum Collection. Collected by H. Klinger.

#### Material

Apart from the holotype, SAS LJE138, SAS A294, A1294, SAS Z8/6 from locality 168 and BMNH C79713 from locality 166 Mfongozi Creek, Zululand. Aptian III-IV.

#### Description

The initial helix is very low and consists of about one whorl. Coiling becomes planispiral at an early stage. The whorl section is rounded throughout.

Ornament consists of very fine ribs, approximately twenty-five per half whorl, separated by interspaces of comparable width. On the earliest whorls preserved, the ribbing is distinctly interrupted over the venter, each rib ending in a minute tubercle on either side of the siphonal line. With increasing diameter, the ventral interruption of ribbing disappears and is present as a mere swelling on each rib along the siphonal line, again creating a 'paternoster' effect. On specimen SAS A1294 (Fig. 79C) ventral tubercles occur on the body chamber on two ribs, separated by five intermediaries.

#### Dimensions

Specimen	D	Wb	Wh	Wb/Wh	U	H
SAM PCZ5682	42	18(42,8)	16(38,1)	1,12	23(50)	14

#### Discussion

The diagnostic characteristics of the species are the fine ribbing and the very shallow helix. Whereas *H. (H) vohimaranitraensis* has about 15 ribs per

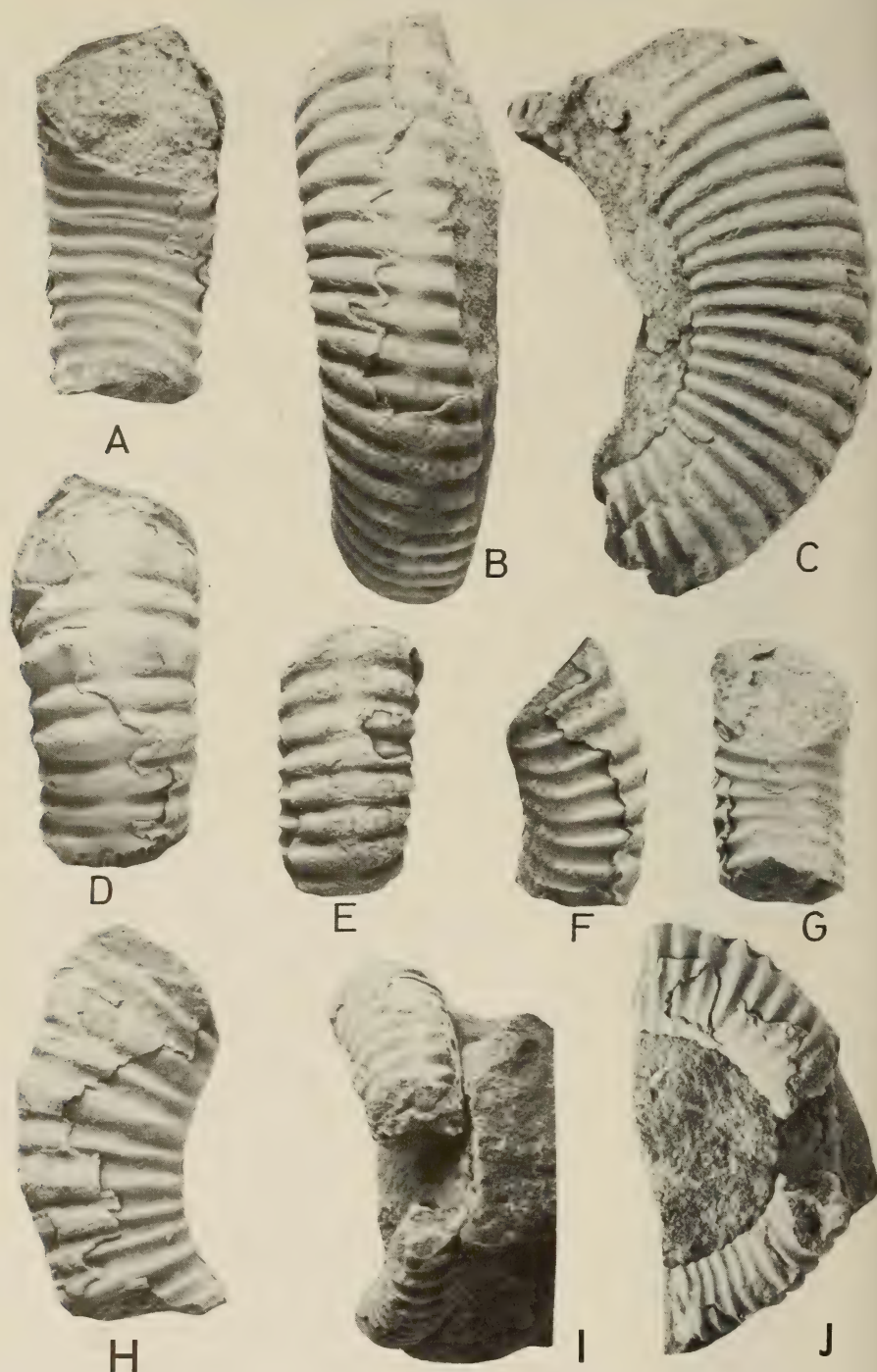


Fig. 75. A, D, H. *Helicancyloceras* (*Nonyaniceras*) sp. indet. BMNH C79698 from locality 166, Zululand, Aptian III.  $\times 2$ . B-C. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). BMNH C79704 from locality 166, Zululand, Aptian III.  $\times 2$ . Transitional to *H. (H.) densecostatum*. E-G. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). BMNH C79705 from locality 166, Zululand, Aptian III. I-J. *Helicancyloceras* (*Helicancyloceras*) *densecostatum* sp. nov. BMNH C79706 from locality 166, Zululand, Aptian III.  $\times 2$ .





A



B

Fig. 76. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). A. SAS H71D/12 from locality 152, Zululand, Aptian IV.  $\times 1,8$ . B. SAS Z8/Hd  $\times 1,5$  from locality 168, Aptian III-IV. Transitional to *H. (H.) densecostatum* sp. nov.  $\times 1,7$ .

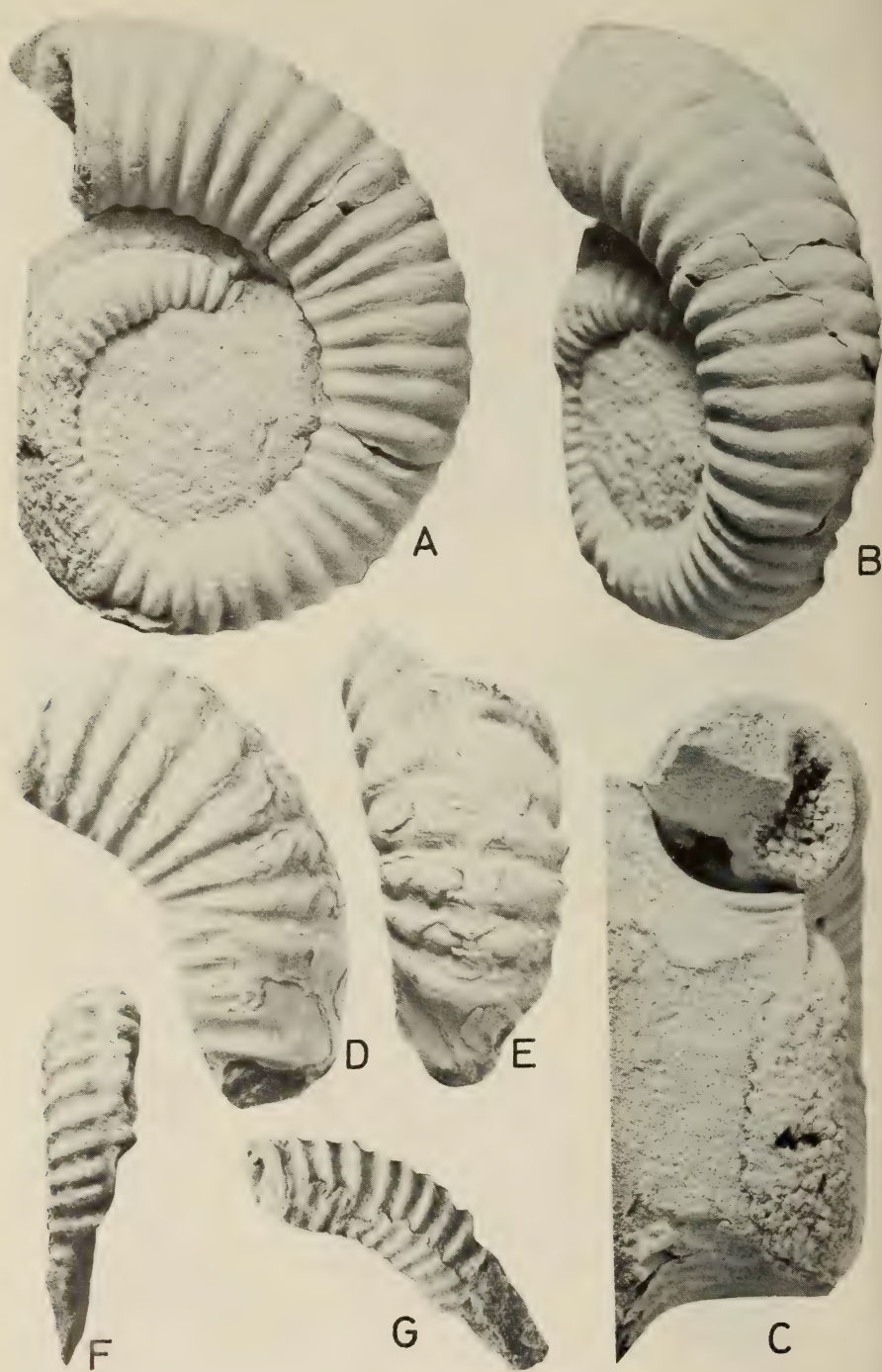


Fig. 77. A-C. *Helicancyloceras* (*Nonyaniceras*) *circulare* sp. nov. BMNH C79708 from locality 166, Zululand, Aptian III.  $\times 2$ . D-E. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis* (Collignon, 1962). BMNH C79710 from locality 166, Zululand, Aptian III.  $\times 2$ . F-G. *Helicancyloceras* (*Helicancyloceras*) sp. indet. BMNH C79693 from locality 166, Zululand, Aptian III.  $\times 2$ .

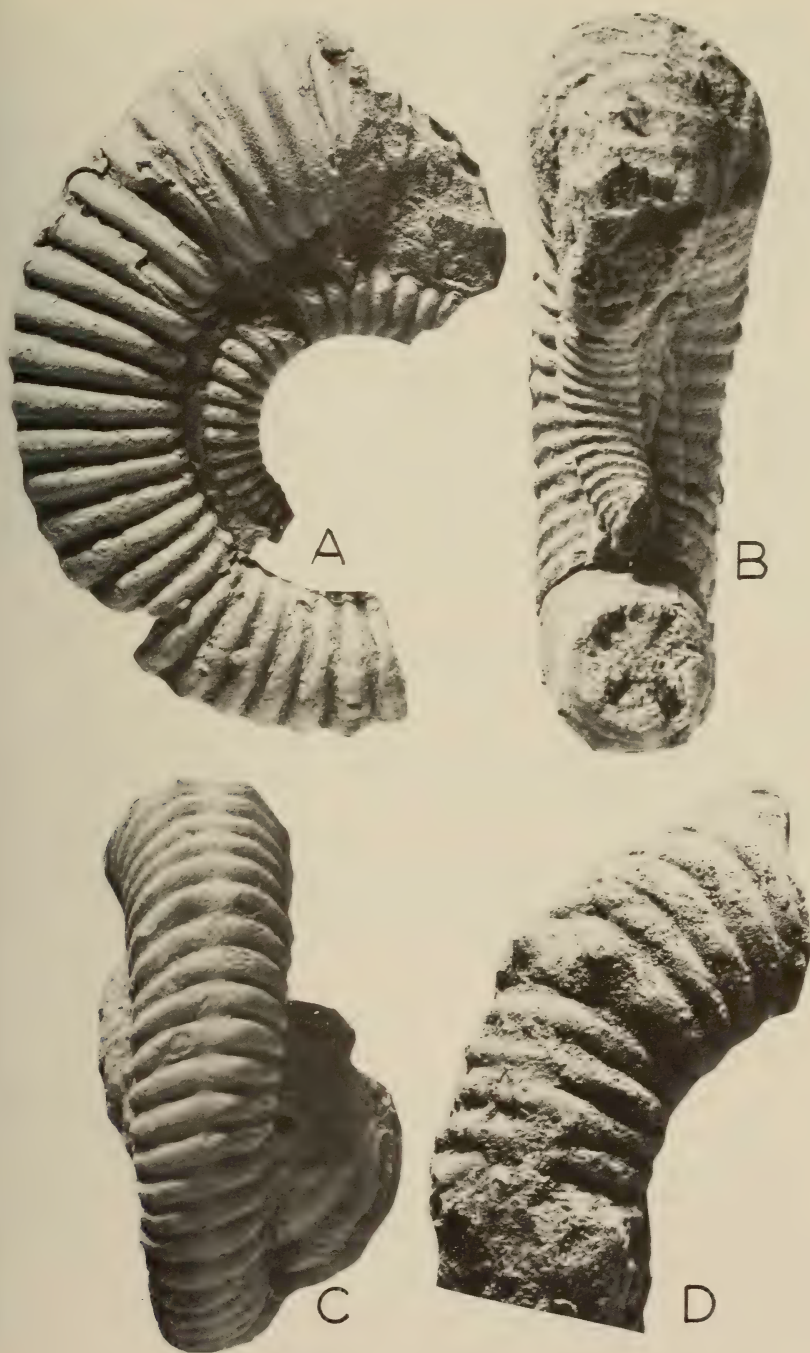


Fig. 78. A-B. *Helicancyloceras* (*Nonyaniceras*) *circulare* sp. nov. SAS H71/2, holotype from locality 151, Zululand, Aptian IV.  $\times 1,5$ . C. *Helicancyloceras* (*Helicancyloceras*) *vohimaranitraensis*. A1924 from locality 168, Aptian III-IV.  $\times 1,5$ . D. *Helicancyloceras* (*Nonyaniceras*) sp. indet. SAM-PCZ5504 from unknown locality, southern part Mkuze Game Reserve.  $\times 1,5$ .



half whorl, *H. (H) densecostatum* has about 25. Transitional forms like SAS Z8/Hd (Fig. 76B) with 21 ribs per half whorl connect the species and may be referred to either. The presence of tubercles on the body chamber of some specimens points to affinities with *H. (Nonyaniceras)*. The presence of tubercles in the very early and late stages with a non-tuberculate middle stage is a situation comparable to that found in *Australiceras*. It is not known if large forms also occur in this species, but the outer whorl is virtually bilateral symmetrical.

#### *Occurrence*

Upper Aptian of Zululand.

#### *Helicancyloceras (Helicancyloceras) spp. indet.*

Several small fragments of heteromorphs with *Helicancyloceras*-like ornament are too poorly preserved for specific identification. A specimen in the collection of the Geological Survey, Z8/21, here figured as Figure 81E is a slightly twisted fragment with the typical ornament over the venter, but does not appear to have been helically coiled. BMNH C79693 is also only slightly curved, indicating looser coiling in, as yet, unknown species of the genus.

#### *Helicancyloceras (Nonyaniceras) nonyani* sp. nov.

Figs 82A–B, 83B

#### *Holotype*

SAS LJE182 from locality 168, Mfongozi Creek, Zululand. Aptian III–IV. Geological Survey Collection. Collected by L. J. Engelbrecht.

#### *Derivation of name*

The species is named for Mr Johannes Nonyane, Klinger's field assistant and laboratory preparator from 1967 to 1975.

#### *Material*

Only the holotype.

#### *Description*

The early whorl forms a very shallow helix, and on the second, and last whorl, coiling is perfectly bilaterally symmetrical at the aperture. The body chamber occupies slightly less than one half of a whorl of the holotype.

The whorl section on the early whorl is round, but becomes ovoid, higher than wide in the body chamber. Initial ornament consists of narrow, rounded radial ribs, separated by interspaces of similar width, each bearing a pair of ventral tubercles. At a diameter of approximately 8 mm, ornament becomes irregular, lateral tubercles appear and the ribs develop a prorsiradial curvature. On the body chamber the ribs pass over the dorsum with a slight forward curvature, but much weakened. The ribs are narrowest at the umbilical edge,

becoming broader towards the venter. Five ribs on the body chamber have prominent ventral tubercles, separated by one to three intermediaries. Lateral tubercles situated on the ventral third of the flanks are developed only on one side, due to injury. Ventral tubercles are variably developed on the intermediaries. They may appear as distinct tubercles or merely as slight edges on the ventrolateral sides of the whorl. The major ribs are slightly thickened and flattened between the lateral and ventral tubercles, and also over the venter, forming incipient loops. Slight thickenings occur between the ribs along the siphonal line, creating a 'paternoster' effect.

### Discussion

The distinct ventral tuberculation and prominent ribbing on the body chamber clearly separates this species from other *Helicancyloceras* and deserves subgeneric rank. The angular costal whorl section on the body chamber is superficially similar to that of *Pedioceras cundinamarcae* Karsten, 1886, from the Barremian of Colombia (see Wright, 1957: L202, fig. 237: 5a-c). That however, is as far as the similarity goes. *Pedioceras cundinamarcae* has a distinct dorsal zone of impression and is coiled planispirally.

### Occurrence

Upper Aptian, Aptian III-IV of Zululand.

### *Helicancyloceras (Nonyaniceras) circulare* sp. nov.

Figs 72A-E, 77A-C, 78A-B

### Holotype

SAS H71/2 from locality 151, Mkuze Game Reserve. Aptian IV. Geological Survey Collection. Collected by H. C. Klinger.

### Material

The holotype and BMNH C79698, BMNH C79708, BMNH 79718 from locality 166, Aptian III.

### Description

The initial helix is very shallow as can be seen in Figure 77A-C, and bilateral symmetry is attained rapidly. The whorl section is circular. Ornament on the inner whorl consists of fine, slightly prorsiradiate ribs, each bearing weak ventral and lateral tubercles. On the outer whorl the ribs are stronger, prominently rounded and separated by narrow interspaces. Two quadrituberculate ribs, separated by three non-tuberculate ribs, are present at the smaller end of the outer whorl of the holotype. The tubercles, lateral and ventral, are very small and pointed.

*Discussion*

The presence of the two rows of tubercles on all ribs of the inner whorl, and the strong, rounded ribbing on the outer whorl, combines features of both subgenera, showing the close relationship between the two. The outer whorl might easily be mistaken for a juvenile *Tropaeum*, as coiling is already planispiral and, unless accompanied by the inner whorls, distinction from *Tropaeum* would be difficult. The very low helix plus the presence of tubercles on the inner whorls and at larger diameters serves to distinguish the species from *H. (H.) vohimarani-traensis*.

*Occurrence*

Upper Aptian of Zululand, Aptian IV.

*Helicancyloceras (Nonyaniceras) crassetuberculatum* sp. nov.

Fig. 79E-F

*Holotype*

SAS L65/13 from locality 168, Mfongozi Creek, Zululand. Aptian III-IV. Geological Survey Collection. Collected by H. Klinger, 1970.

*Material*

Apart from the holotype, SAS L65/14 from the same locality.

*Description*

The holotype consists of half a whorl. The whorl section is rounded. The original helix must have been very shallow, but the helical coiling is nevertheless rendered distinct by the asymmetry of ornament over the venter. Ornament consists of major trituberculate ribs, separated by one to three narrower intermediaries. The umbilical tubercles are smallest, and virtually absent at the smallest diameters visible. The ventrolateral and ventral tubercles are conical, very prominent, and situated close together. On the flanks the trituberculate ribs show signs of flattening or duplication. Ribbing is weakened on the dorsum, and the major ribs duplicate at larger diameters. The intermediary ribs are weakly tuberculate over the venter at small diameters. With increasing diameter the tuberculation becomes less noticeable.

*Discussion*

*H. (N.) crassetuberculatum* is distinguished from other species of the subgenus by the very prominent tuberculation at small diameters. Fragments bear similarity to *Ancyloceras*, but the asymmetry of ornament over the venter reveals the generic affinity.

Anderson's *Helicancylus gabbi* (1938: 222, pl. 79 (figs 4-5)) is a similar helical form of uncertain generic affinity. The ribbing, however, is much stronger and there are fewer intercalatories. As yet the systematic position of



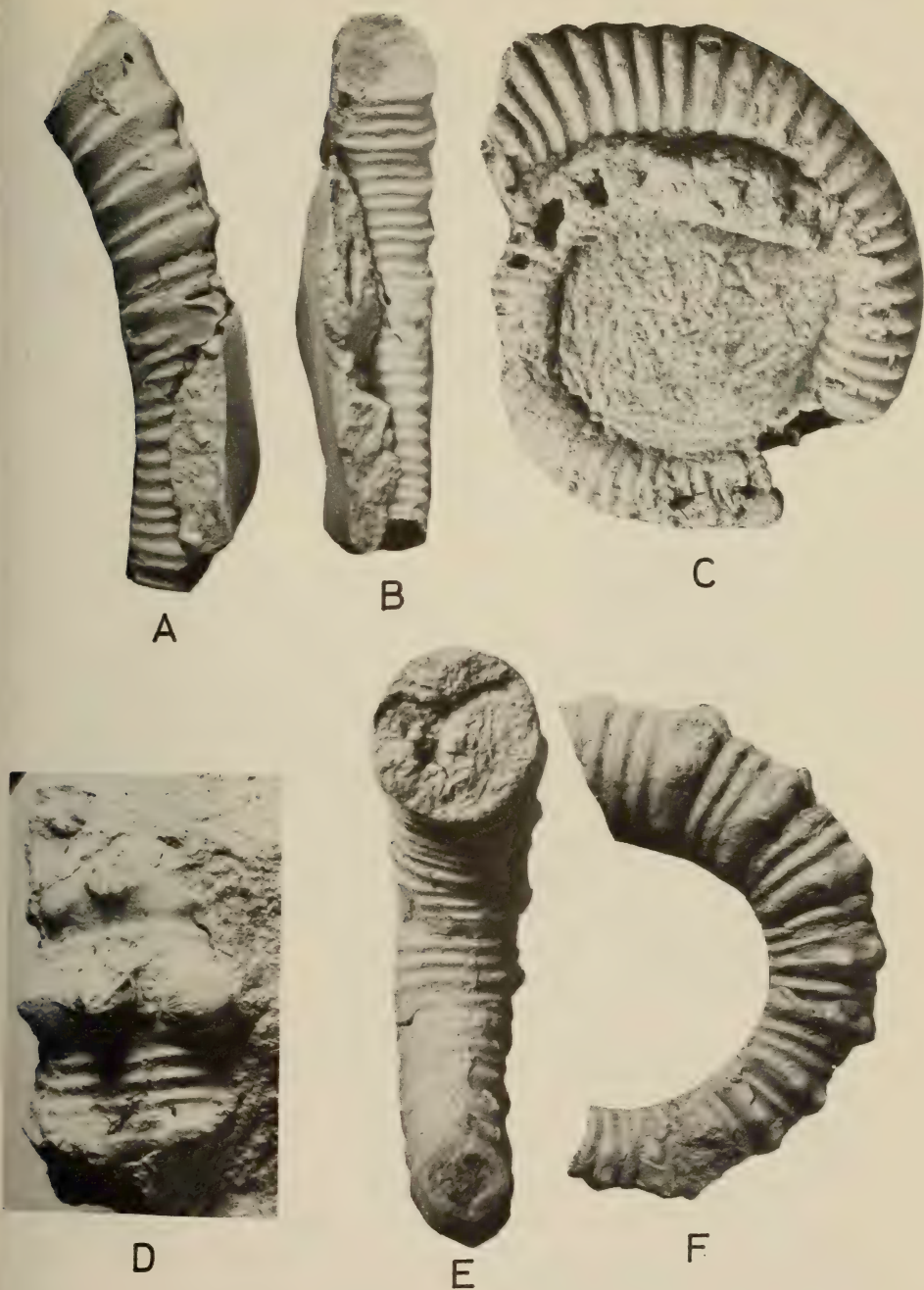


Fig. 79. A-B. *Toxoceratoides? haughtoni* sp. nov. SAS Z8/Ti from locality 168, Zululand, Aptian III-IV.  $\times 1,6$ . C. *Helicancyloceras* (*Helicancyloceras*) *densecostatum* sp. nov. SAS A1294 from locality 168, Zululand, Aptian III-IV.  $\times 1,55$ . D. *Ancyloceras* (*Ancyloceras?*) sp. indet. SAS H54/39 from locality 170, Zululand, Aptian I.  $\times 1,5$ . E-F. *Helicancyloceras* (*Nonyaniceras*) *crassetuberculatum* sp. nov. SAS L65/13, holotype from locality 168, Zululand, Aptian III-IV.  $\times 1,5$ .

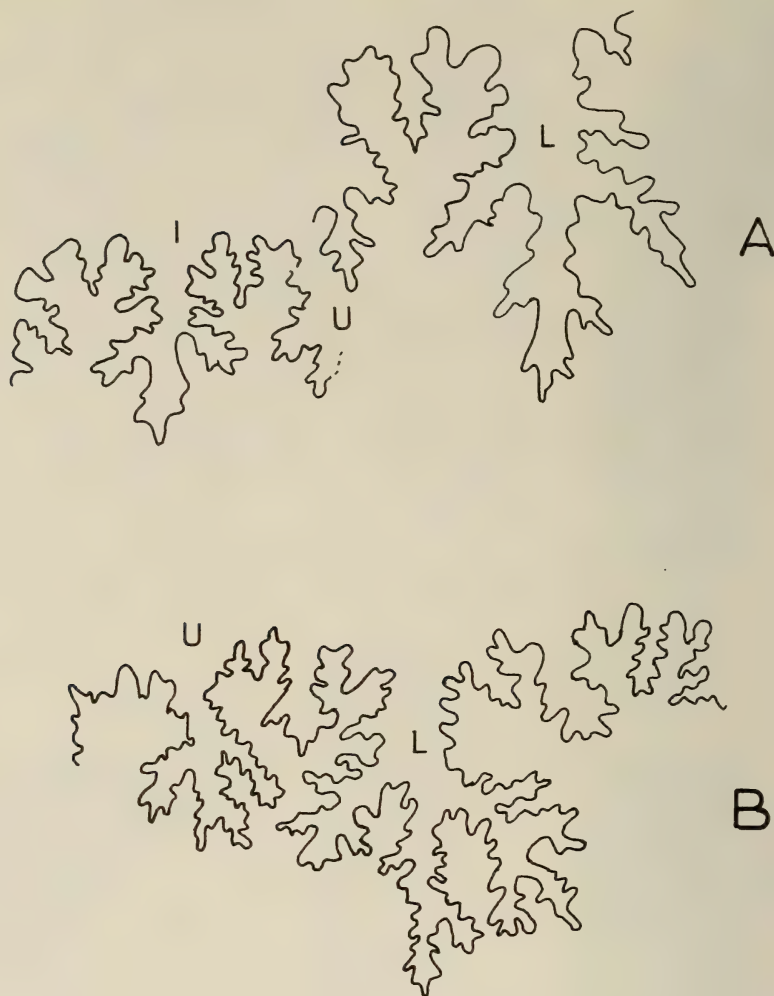


Fig. 80. A. Suture line of *Australiceras* sp. aff. *irregulare* (Tenison Woods, 1883). SAM-PCZ5506.  $\times 3$ . B. Suture line of Z8n, Insertae sedis.  $\times 1$ .

this species is not known, and it is not certain if the specimen is congeneric with the hamulinid *Helicancylus aequicostatus* (Gabb).

*Ancyloceras helicoides* Rouchadzé (1933: 17, pl. 8 (fig. 3) is another ancyloceratid form, but again the tuberculation is much stronger and is referred to *Kutatissites* of Late Barremian age.

#### Occurrence

Upper Aptian of Zululand.